

SILICIFIED BRACHIOPODS FROM
THE VISEAN OF COUNTY
FERMANAGH (II)



BY
C. H. C. BRUNTON x-ref.

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SILICIFIED BRACHIOPODS FROM THE VISEAN OF COUNTY FERMANAGH (II)

By C. H. C. BRUNTON

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SYNOPSIS

This paper, the second of a series describing the Viséan brachiopods from near Derrygonelly in county Fermanagh, deals with the Inarticulata, Enteleteacea, Strophomenacea, Davidsoniacea and Chonetacea. *Brochocarina* and *Serratocrista* are new Davidsoniacean genera and *Globosochonetes* a new chonetid genus; four new species are described. Additional evidence is presented for the separation of *Leptagonia* from *Leptaena* and the relationship of the Chonetacea to the Productacea is discussed.

I. INTRODUCTION AND ACKNOWLEDGMENTS

THIS study follows that of the Productacea (Brunton 1966) as part of a series dealing with the brachiopods etched out with acid from Viséan limestones at the Sillees river near Bunnahone Lough, or on the southern shore of the nearby Carrick Lough, about 2 miles N.W. of Derrygonnelly in county Fermanagh, Northern Ireland. All the material is from these localities unless otherwise stated in the text, and is of a Low D zone age. A locality map was given in the previous part (Brunton 1966; 178, fig. 2).

I take pleasure in thanking Professor A. Williams for his help and encouragement while engaged upon much of the work in his department during the tenure of a D.S.I.R. studentship. I am grateful to Dr. H. M. Muir-Wood, late of the British Museum (Natural History); Dr. I. Rolfe, Hunterian Museum, Glasgow; the late Professor R. G. S. Hudson, Trinity College, Dublin; Dr. G. A. Cooper, Smithsonian Institution, Washington; Dr. K. E. Caster, University of Cincinnati; Mr. J. M. Edmonds, University Museum, Oxford and Mr. M. Mitchell, Institute of Geological Sciences, London for the loan of specimens in their care and for advice. Some of the photographs were taken by members of the Photographic Department of the British Museum (Natural History); to them and many other helpers I extend my thanks.

I am grateful for having had my attention drawn to the fact that in my previous publication upon the Productacea (1966) I did not make clear from which locality new taxa were collected. The information is given below:

Dasyalosia panicula Brunton: Carrick Lough.

D. lamnula Brunton: Bunnahone.

Krotovia lamellosa Brunton: Bunnahone.

Eomarginifera (Eomarginiferina) trispina Brunton: Bunnahone.

II. SYSTEMATIC DESCRIPTIONS

Unless otherwise stated the majority of the specimens here described were collected from the Sillees River locality (Irish Grid Reference 2105 : 3550): other specimens are from the Carrick Lough locality (Irish Grid Reference 2092 : 3538). The fauna from these localities (separated by a distance of 1 mile) are considered to be of the same age (low D Zone).

All specimens prefixed by B or BB are in the collection of the British Museum (Natural History). The depository of other specimens is given in the text.

Class *INARTICULATA*

Suborder CRANIIDINA Waagen 1885

Superfamily CRANIACEA Menke 1828

Family CRANIIDAE Menke 1828

Genus *CRANIA* Retzius 1781

TYPE SPECIES. *Anomia craniolaris* Linné, by subsequent designation of Schmidt (1818 : 71).

Williams (1943 : 70) erected the subgenus *Lissocrania* for "Cranias with dorsal valves devoid of radial costae or spines. Ornamentation, if any, consists of con-

centric growth lines or of fine radiating striae or both." The type species, *Crania dodgei* Rowley is poorly known and its interior was not described by Rowley (1908), Weller (1914) or Williams (1943). The type species of *Crania* s.s., from the Cretaceous, and the modern *C. anomala* (Müller) are devoid of radial ribbing and may have slightly larger dorsal posterior adductor scars than anterior scars. Thus, with our present knowledge, the retention of *Lissocrania* is unjustified, and in the recently published Brachiopoda Treatise (1965) it is tentatively placed in synonymy with *Crania*.

Other non-ribbed craniid genera are *Petrocrania* Raymond 1911 (= *Craniella* Oehlert 1888) and the poorly known genus *Philhedrella* Kozłowski 1929, originally erected as a subgenus of *Philedra*. Distinction between these two genera may lie in the presence of well defined dorsal mantle canal traces in *Petrocrania* and in its dorsal posterior adductor scars being larger than the anterior scars, apparently unlike *Philhedrella*. In his revision of craniids von Huene (1899) included *C. quadrata* (M'Coy) and *C. kirkbyi* Davidson in *Craniella* (now *Petrocrania*), but as this group is not known to possess sigmoidal mantle canal traces in the dorsal valve they should probably be removed from *Petrocrania*. Conceivably they could be assigned to *Philhedrella* or *Crania*. Species at present within *Philhedrella* range from the Ordovician to Upper Silurian, while *Crania* species are described from the Carboniferous times up to the Recent. As the former genus is inadequately known *Crania* is perhaps the more appropriate genus within which to place *C. quadrata*, the species to which the smooth-shelled Fermanagh craniids are assigned.

There are marked differences in the morphology of Carboniferous and Cretaceous *Crania*. The Mesozoic forms are thick shelled with deeply impressed muscle scars, particularly those of the pedicle valve which are cavernous in form, and a limbus is common. Palaeozoic shells are thin and the muscle scars are commonly raised areas in both valves; the brachial valve is without the internal radial ridges seen between the muscle scars of the Mesozoic forms. Such differences may result from a greater ability of Mesozoic shells to deposit skeletal material and it may prove more realistic to distinguish the Palaeozoic species as a group. A clear understanding of *Philhedrella* may reveal that this genus would be suitable for some non-ribbed Palaeozoic species presently assigned to *Crania*.

Crania quadrata (M'Coy)

(Pl. 1, figs. 1-9)

1844 *Orbicula quadrata* M'Coy: 104, pl. 20, fig. 1.

1861 *Crania quadrata* (M'Coy) Davidson: 194, (1863) pl. 48, figs. 1-13.

1899 *Craniella quadrata* (M'Coy) Huene: 148.

DESCRIPTION. Outline irregular, rounded to subquadrate when undeformed, with gently folded margin, posteriorly flattened to gently sulcate; ventral valve entirely fixed; dorsal valve subconical with beak directed posteriorly and closer to posterior margin; ornamentation of concentric growth lines and scattered short spine-like protuberances, valve margins may be slightly thickened; dorsal anterior adductor

scars close to apex, separated by distance equal to width of scar and from less distinct, widely spaced posterior scars situated close to valve margin; slight radial ridge from beak to valve edge between the muscle scars; shell substance punctate.

MEASUREMENTS (in mm.):

	length	width
Incomplete brachial valve (BB.55599)	c. 16.5	c. 20.0
Complete brachial valve (BB.55600)	7.5	8.6
Complete brachial valve (BB.55601)	3.7	3.9
Complete brachial valve (BB.55602)	2.2	2.3
Complete brachial valve (BB.55603)	2.1	2.4
Incomplete brachial valve (BB.55616)	2.1	1.2

DISCUSSION. The fauna from Fermanagh includes a wide range of sizes, from about 1.0 mm. to an incomplete brachial valve about 20.0 mm. wide. Pedicle valves are absent from the collections. Among the juvenile valves are some small shells of up to 5 mm. long which are almost as high as long and which have well defined narrow posterior trigonal areas. Together with these highly conical valves are more typically proportioned specimens looking more like the larger specimens. It may be that different habitats induced differing juvenile forms or that we have in the collection a different species, only represented by these small shells. An example of these conical forms is figured (Pl. 1, figs. 6, 7). Normally the larger valves are about one-half as high as long.

Valve outline is variable, depending upon the shell's site of attachment and probably upon its degree of crowding, but one well formed specimen, with a high degree of bilateral symmetry may be taken as being typical of undeformed specimens (Pl. 1, figs. 4, 5). The posterior trigonal area is differentiated by a pair of shallow sulci extending from the beak to the valve margin. Anteriorly the margin is slightly bilobed as a result of a third antero-median shallow groove. These features, together with the more posteriorly placed beak, give the valves a distinct orientation. Although appearing smooth externally, save for a few growth-lines, these valves are also ornamented by sparsely scattered more or less concentrically arranged spine-like protuberances. The possibility that these structures are an artifact of the silicification process has been recognized, but rejected on account of their regular development upon the specimens available. Rarely these "spines" can be seen to project at a high angle from the surface, but only for about 0.1 mm., and they are spaced about 0.4 mm. apart. This is considerably more widely scattered than are the "spines" of *Acanthocrania*.

Internally the anterior muscle scars are situated towards the top of the trigonal posterior region, on the slight infolds of the valve, and extend for nearly one-half of the distance towards the margin. The smaller, more rounded posterior scars are not radially aligned with the anterior scars and are only slightly more widely spaced. Dividing the trigonal area is a slight median thickening which is most clearly developed near the somewhat thickened valve margin.

In 1858 Davidson erected the species *Crania kirkbyi*, from the Permian of N.E. England, which he described as being "... sub-quadrate, with rounded angles, and is sometimes a little indented at its anterior margin". Davidson continued by saying that the external surface was closely covered by a multitude of minute, short, hollow, spinose tubercles, which produce a granulated aspect." (1858 : 49). The interior was poorly described. In 1863 Davidson added a note upon the species saying that he thought the granulation was unnatural and that his species may be the same as *C. quadrata* (M'Coy) from the Carboniferous. He figured the two species on plate 54 (1863) and the two appear identical. If Davidson's first impressions regarding the granulated looking surface of *C. kirkbyi* were correct it would seem even more likely that the two are conspecific.

Genus *ACANTHOCRANIA* Williams 1943

TYPE SPECIES. *Crania spiculata* Rowley (1908), by original designation of Williams (1943 : 71).

Acanthocrania cf. *laevis* (Keyes)

(Pl. 1, figs. 10-14)

1894 *Crania laevis* Keyes: 40.

1914 *Crania laevis* Keyes; Weller: 47, pl. 1, fig. 33.

DESCRIPTION. Outline transversely elliptical with flattened posterior margin; ventral valve unknown; dorsal valve deep, lateral profile asymmetric, anteriorly evenly convex, posteriorly steep to concave; beak posteriorly directed and may be below valve apex; ornamentation of sporadic sublamellose growth-lines and closely spaced radially directed spines at low angle to valve surface, arranged more or less concentrically and quincuncially; adductor scars divided, anterior pair just posterior of valve apex, near beak, similarly sized posterior scars close to valve margin and widely separated; shell substance punctate.

MEASUREMENTS (in mm.)

	length	width
Complete brachial valve (BB.55604)	4.6	5.7

DISCUSSION. Wright (1963 : 249) discusses the genus mentioning its range from the Ordovician to the Carboniferous. The first record of the genus from the British Isles is that of Wright for Ashgillian specimens from the Portrane Limestone of Co. Dublin. The type species is a North American Visean form and this Fermanagh record is the first from the upper Palaeozoic of the British Isles.

The specific description of *A. laevis* given by Keyes is inadequate and the species not illustrated. However, Weller (1914) gave a full description, with a figure, of the specimen from "... the Burlington Limestone ... used by Keyes", and from

this it is clear that it is closely comparable to the Fermanagh material. The specific name given by Keyes (1894) is inapt but possibly results from the lectotype being silicified and the papillose surface being thought to result from this process. Keyes noted that the surface was "marked by concentric lines of growth", but it was Weller who described the papillose or spinose nature of the surface. This external ornamentation is well preserved on the few valves available from Fermanagh and near the margins, where the "spines" are longest, they are up to 0.4 mm. long. These papillae or spines may be morphologically associated with the shell punctation, which is only clearly visible on the internal surfaces of the Fermanagh specimens. The spines arise from the shell in positions corresponding to the internal positions of punctation and both have similar numbers per unit area, although there are commonly rather more spines. This may result from the coalescence of several juvenile punctae into a single larger puncta within younger parts of the shell. This has been described previously in *Crania* (e.g. Joubin, Blockman) and recently re-figured by Rowell (in Williams *et al.* 1965, fig. 77).

Weller's description (1914 : 48) of the brachial valve interior of the American material is accurate for the present specimens and the widely spaced posterior adductor scars are slightly larger than the closely and apically placed anterior scars. The posterior scars are less well defined and it is likely that with age they would have grown more prominent and proportionately still larger than the anterior scars. The margins of the valve are not greatly thickened although slight lamellae were developed.

As there is only one complete specimen, together with fragments, it is impossible to present variation studies on this species. Rarely the brachial valve may have grown in a distorted fashion and may show signs of the skeletal material against which it grew.

Genus *PHILHEDRA* Koken 1889

TYPE SPECIES. *Philhedra baltica* Koken by original designation of Koken (1889: 465).

Philhedra trigonalis (M'Coy)

(Pl. 1, figs. 15-29)

1844 *Orbiculata trigonalis* M'Coy: 401, pl. 20, fig. 2.

1899 *Philhedra trigonalis* (M'Coy) Huene: 147.

DESCRIPTION. Outline subrounded to longitudinally subelliptical; profiles asymmetrical and variable with beak posterior of mid-length and at apex of valve; margins of brachial valve irregularly shaped through contact with substrate; growth-lines distinct and commonly interrupting radial ribs which extend from near apex to valve margins, ribs increase in width and added by branching and rare intercalation; brachial valve interior with anterior adductor scars slightly raised, oval, closely placed near beak and divergent towards less distinct ovoid posterior scars

which extend close to valve margin; pedicle valve thin and poorly known, with growth-lines and distorted to conform to object of attachment; shell substance punctate.

MEASUREMENTS (in mm.)

	length	width
Complete brachial valve (BB.55608)	11.0	8.4
Incomplete brachial valve (BB.55609)	11.4	c. 7.5
Complete shell attached to rugosochonetid (BB.55607)	8.5	7.5
Complete brachial valve (BB.55610)	8.0	6.7
Distorted brachial valve (BB.55611)	6.9	7.4
Incomplete shell (BB.55612)	5.7	5.6
Complete brachial valve (BB.55613)	4.0	4.2
Complete brachial valve (BB.55614)	2.7	2.5

DISCUSSION. The Fermanagh sample is varied in size (having a range of from 2.0 mm. to 12.0 mm. long) and outline. The beak is asymmetrically placed and the height of the shells differs from just under one-half to less than one-quarter of the shell length. Ventral valves are rarely preserved and their interiors have not been observed. However, it is clear that these valves were much effected by the substrate; they commonly show growth-lines and are punctate.

The dorsal valve is rounded to subelliptical in outline with little or no posterior flattening, as is common in *Acanthocrania* and *Philhedrella*. The posterior slope is less steep than in these genera although the beak is posterior of mid-length. The larger shells are more elongate than the smaller ones and in profile they retain their height for a short distance before dropping to the anterior margin (Pl. 1, fig. 17). The costae arose within about 1 mm. of the beak and costellae were added by unequal branching or intercalation. The rib crests are somewhat serrated and commonly interrupted by the growth-lines; their width increases slightly towards the valve margins. Some shells became distorted from growth against foreign objects, such as fenestellid colonies, (Pl. 1, fig. 25) and the substrate upon which the shells grew had a marked effect upon the shape of the commissure.

Apart from the adductor scars and punctae the brachial valve interior is devoid of structures. In the present silicified material the punctae are most clearly developed and largest close to the valve margins. One valve has a tent-like ridge anterior of the beak and oblique to the mid-line (Pl. 1, fig. 29). The antero-lateral end of this ridge appears to be broken and there is nothing to suggest that there was another ridge on the opposite side of the shell or that damage to the shell resulted in its formation.

The distinction between *Crania* and *Philhedra* rests principally upon the relative sizes of the muscle scars in the dorsal valve and external ornamentation; *Philhedra* being distinguished as having larger anterior scars than posterior scars and better defined costellate ribbing.

Class *ARTICULATA*

Order ORTHIDA Schuchert & Cooper 1932

Superfamily ENTELETACEA Waagen 1884

Family ENTELETIDAE Waagen 1884

Subfamily SCHIZOPHORIINAE Schuchert & Le Vene 1929

Genus *SCHIZOPHORIA* King 1850

TYPE SPECIES. *Anomites resupinatus* Martin 1809, by original designation of King (1850 : 106).

George & Ponsford (1938 : 228) selected a neotype for *S. resupinata* (Martin) and this specimen (BM(NH) BB.2420) was later figured by Bond (1942, pl. 21). The specimen is large; 55.5 mm. long, 72 mm. wide and 32.5 mm. thick, and as Bond said "would approach Demanet's variety *gigantea*" (Pl. 2, figs. 1-3). The Fermanagh shells range in length from 1 mm. to 13.5 mm. and never display the resupination of the pedicle valve commonly seen in large specimens, such as the neotype.

In his study of Carboniferous *Schizophoria* Bond (1942, for 1941) divided the British and Belgium species into those with coarse ornamentation, i.e. with 3 or 4 ribs per mm. about 10 mm. from the umbo, and those species with fine ribbing, i.e. 6-9 ribs per mm., 10 mm. from the umbo. Into the former group he placed *S. resupinata* and its varieties *gigantea* Demanet, *dorsosinuata* Demanet, *lata* Demanet, *pinguis* Demanet, *rotundata* Demanet, and *elboltonensis* George & Ponsford, (which are further united by having dental plates at about 70° from one another) together with the species *S. nuda* George & Ponsford, *S. hudsoni* George and *S. connivens* (Phillips). The type specimen of Phillips' species is lost and his figure (1836, pl. 11, fig. 2) is inconclusive. However, Bond selected a neotype from among specimens in the Gilbertson Collection in the British Museum (Nat. Hist.) (B.387, re-registered as BB.54902) which is distinguished from *S. resupinata* by its more globose profile, near sulcinate anterior commissure, short hinge line, narrowly divergent dental plates (30°) and small size (16 mm. long). However, Bond admits that only one specimen with such a commissure was seen in his study and that its shape variants grade into some of the more rounded and globular variants of *S. resupinata*. The dental plates are said to be a valid distinction. This being so the Fermanagh shells can not be attributed to *S. connivens* as their dental plates diverge at about 70°, like *S. resupinata* s.s.

George & Ponsford (1938) spoke of *S. dorsosinuata* Demanet as a distinct species and illustrated sections of three specimens that they attributed to Demanet's variety. Two of these illustrations (1938, figs. 11, 14) are of interest in that the brachiophore bases are at an angle to the brachiophores, as are those of the Fermanagh shells. Serial sectioning has confirmed this feature in a toptype specimen of Demanet's var. *dorsosinuata* from Tournai, Belgium (kindly presented by Dr. P. Sartenaer) and has led me to assign the Fermanagh specimens to what I consider

the subspecies *S. resupinata dorsosinuata* Demanet. The brachial valve of the neotype is sulcate for approximately the first 50 mm. of its length. This dorsal sulcation is not a common feature but when present most probably produced a unisulcate anterior commissure, similar to that of the present material, before the onset of resupination of their pedicle valves.

Schizophoria resupinata (Martin) *dorsosinuata* Demanet

(Pl. 2, figs. 7-37; Text-figs. 1-4)

- 1861 *Orthis resupinata* (Martin) Davidson (pars.): 130, pl. 30, fig. 1, non figs. 2-5.
 1934 *Schizophoria resupinata* var. *dorsosinuata* Demanet: 53, pl. 3, fig. 14, 15.
 1938 *Schizophoria* cf. *dorsosinuata* Demanet; George & Pensford, figs 11, 14.
 1942 *Schizophoria resupinata* var. *dorsosinuata* Demanet; Bond: 289.

DIAGNOSIS. Small, biconvex dorsally sulcate *Schizophoria* with unisulcate anterior commissure; brachiophores subparallel but brachiophore bases diverging to valve floor.

DESCRIPTION. Outline rounded subrectangular, length about four-fifths maximum width, hinge-line straight, about one-half width, cardinal extremities rounded, anterior margin gently rounded to emarginate and commissure slightly unisulcate; profile biconvex, depth about one-half length, increasing with age; gentle dorsal sulcation; radial ornament of low rounded and delicate ribs, about 14 in 2.5 mm. at 5 mm. antero-medially from dorsal umbo, about 10 costae and first order costellae commonly remaining prominent; branching by intercalation and rib apertures well developed; concentric ornament sporadic but distinct; ventral interarea concave, apsacline, delthyrium triangular, open; dorsal interarea about one-half length of ventral interarea, curved anacline, with open notothyrium, chilidium obsolete; teeth strong, triangular in outline and diverging at about 45° from mid-line, supported by receding divergent plates fused posteriorly to inner surfaces of umbonal slopes; notch below teeth articulating with apophyses on brachiophores; base of dental plates extending anteriorly as ridges laterally enclosing oval muscle scars about two-fifths valve length; muscle field width about three quarters its length and medianly divided by strong anteriorly widening ridge on antero-lateral faces of which are narrow lanceolate adductor scars; mantle canal traces obscure, but pair of strong *vascula media* extend anteriorly from anterior ends of each diductor scar; cardinal process developed as ridges across floor of notothyrial cavity, between brachiophore bases, with distally expanded and incised myophore, trilobed in adults; brachiophores strong, diverging at about 40° from mid-line, median faces vertically disposed and fulcral plates well developed; brachiophore bases diverging to valve floor, continued anteriorly as indistinct ridges surrounding adductor field but interrupted by traces of three mantle canals; adductor field about four-ninths valve length and about as long as wide, divided medianly and into posterior and anterior scars; marginal follicular embayments may persist posteriorly.

MEASUREMENTS (in mm.)

	length	width
Complete shell (BB.52701)	13·8	16·0
Complete shell (BB.52702)	13·0	—
Pedicle valve (BB.52703)	11·3	14·5
Incomplete brachial valve (BB.52705)	12·5	—
Complete brachial valve (BB.52707)	3·1	3·7
Complete brachial valve (BB.52708)	3·8	4·6
Complete brachial valve (BB.52709)	5·5	6·7
Incomplete brachial valve (BB.52711)	c. 16·0	—
Complete pedicle valve (BB.52713)	2·0	2·6
Complete pedicle valve (BB.52714)	7·0	8·5
Incomplete brachial valve (BB.52715)	c. 11·5	—
Complete shell (BB.52716)	2·9	3·6
Complete shell (BB.52717)	1·3	1·6

DISCUSSION. The present Fermanagh *Schizophoria* specimens accord most closely with Demanet's variety from the Tournaisian of Belgium. Similar specimens were described by Sanders (1958 : 43) from rocks of Kinderhook age in Mexico under the new name *S. sulcata*. This silicified material shows interiors comparable to those from Fermanagh although the Mexican shells are about 10 mm. longer and relatively thicker. The cardinal process's of both faunas are comparable in having a bifid central lobe and a pair of lateral lobes within the notothyrial cavity (Sanders 1958, pl. 3, fig. 19, cf. Pl. 2, fig. 17). Sanders characterizes his species by "the sulcus on each valve", (p. 44) but only that on the dorsal valve is clear from his figures.

The external radial ornamentation arose from the initial 10 or 12 costae by the apparent intercalation of costellae, mostly posteriorly. The costae arose within 0·3 mm. of the umbones of each valve. The brachial valve commonly had a median costa for about the first 3 mm. of growth which subsequently was usually diverted to one side of the median sulcus. First order costellae were added at about 0·5 mm. and second order costellae may show at a length of 1·5–2·0 mm. These additions appear as intercalations, but on close study it is usually possible to determine from which parent rib the costella had arisen, and in this way it can be seen that there is a tendency towards median branching across the sulcus and lateral branching on the dorsal flanks. On pedicle valves lateral branching is more common in a manner similar to that illustrated by Williams & Wright (1963 : 23). Biernat (1959 : 61) records 12 ventral and 13 dorsal costae on *S. striatula* from the mid-Devonian of Poland. These arose at a length of about 0·45 mm. and with a further 0·5 mm. of growth both first and second order costellae arose. On young specimens a few mm. long, only the apical tips of the beaks are free of costae and these areas represent the brephic valves and protegular nodes. On Fermanagh shells the ribs are low and rounded and increase in size only slightly towards the anterior margins so that 2, 6, 8, 3 and 1 specimens have respectively 12, 13, 14, 15 and 16 ribs in 2·5 mm. at a distance of 5 mm. from the dorsal umbo. Along the costae and primary costellae,

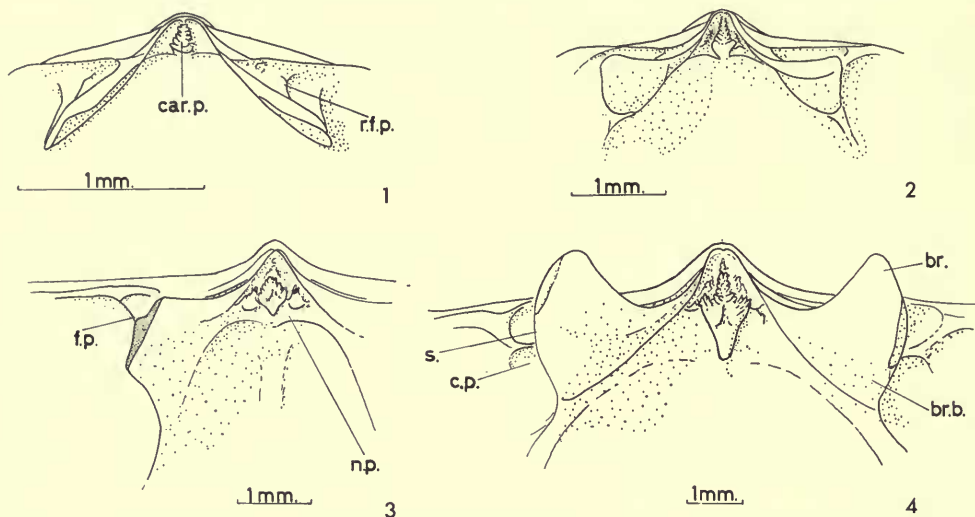
which commonly remain rather larger than the intervening ribs, rib apertures ("hollow costellae" of Schuchert & Cooper, 1932 : 143) occur 3 or 4 times per 10 mm. length. This frequency appears to be less than illustrated by Davidson (1861, pl. 30, fig. 1d) or Sanders (1958, pl. 3, fig. 22) but is probably the result of their increased occurrence with age and size of the shell. These apertures have been interpreted as small spine bases viz. Davidson (1861 : 130), Dunbar & Condra (1932 : 54 and Cvancara (1958 : 857). Demanet figures what he describes as an external impression of a brachial valve (1934, pl. 3, fig. 13) of *S. resupinata* var. *rotundata* Demanet showing minute needle-like rods of iron oxide extending away from the mould into what must have been shell substance. Demanet (1934 : 52) is undoubtedly correct in interpreting these minute rods as being infillings of the shell punctae. There is no clear evidence yet available indicating the significance of the rib apertures. If, however, their open nature at the valve margins, prior to secondary shell deposition, indicates a functional origin at the mantle margins, it seems likely that the apertures may have assisted in the sensory apparatus of the shell in a way comparable to the "sensory" spines described by Rudwick (1965 : 610). The development of the ventral interior can be traced readily from valves of less than 2 mm. long, by which stage the bilobate muscle field was well developed (Pl. 2, fig. 32). The teeth were not differentiated from the interarea until the valve was about 6 mm. long, but the dental plates were already strongly formed and fused with the inner surfaces of the valve posteriorly. Only along their anterior margins did the dental plates remain discrete from the valve. The ridges enclosing the lateral margins of the muscle field were developed by this stage, as was the strong median ridge, but differentiation within the muscle field is impossible to distinguish. Indeed, it is commonly impossible to see the narrow adductor scars on the median ridge or the narrow lateral lobes of the diductor scars even on the largest shells available. The ventral adjustor scars are rounded trigonal markings upon the inner surfaces of the dental plates.

The coefficients of correlation for all measured parameters are high (see Tables 1, 3) indicating a regular proportional growth. The increased curvature anteriorly of the brachial valve results in an allometric effect for length relative to width ($p \leq 0.01$), but is not apparent in the sample for other paired parameters. In his studies of *S. resupinata* s.l. from the Lower Carboniferous reefal limestones of northern England, Parkinson (1954) illustrates a possible allometric change in the growth ratios of plots of thickness against length or width at a shell width of about 20 mm. As has been pointed out by Veevers (1959), allometry cannot be clearly indicated without tests of significance having been applied to differing sectors of the growth axis, and this Parkinson did not do.

The shallow dorsal sulcus became distinguishable in valves about 3 mm. long, but became prominently developed between 5 and 10 mm. from the umbo and persisted to the anterior margin. Internally the dorsal muscle field is discernible in shells about 2 mm. long, as is the small knob-like cardinal process and, rarely, the two median mantle canal traces. When the valve was about 3 mm. long a small ridge started to develop on the postero-lateral surfaces of the brachiophores, within the sockets, which grew anteriorly to form fulcral plates. These were not sufficiently

developed to arch the crural pits until the valve was about 5 mm. long. At this stage the brachiophore tips were about 2 mm. apart, and although the median ridge had not yet developed between the adductor scars, they were divided into anterior and posterior scars by a laterally directed pair of mantle canals (Pl. 2, fig. 30).

The growth of the cardinal process took place from the apex of the notothyrial chamber as a longitudinally disposed ridge, to the ventral surface of which were attached the diductor muscles. The ridge was not divided distally into myophore lobes, as is commonly found in adult dalmanellids, and the muscle bases presumably extended along its length and onto its flanks. (Text-fig. 1). Shell thickening at the



FIGS. 1-4. Illustrations of the ontogeny of the cardinalia of *Schizophoria resupinata dorsosinuata* Demanet showing the development of the trilobed cardinal process from the notothyrial platform; *br.*, brachiophore; *br.b.*, brachiophore base; *car.p.*, cardinal process (juvenile primary lobe); *c.p.*, crural pit; *f.p.*, fulcral plate (in Fig. 3 the brachiophore tip is not drawn so as to reveal the fulcral plate); *n.p.*, notothyrial platform; *r.f.p.*, rudimentary fulcral plate on juvenile specimen; *s.*, socket.

base of the cardinal process built a notothyrial platform, distinguishable in valves about 6 mm. long. This platform remained sunk below the dorsal interarea and even in adult Fermanagh shells was no more than 1 mm. long. During growth the diductor muscle bases must have spread laterally onto a pair of ridges (Text-figs. 2, 3) which developed from the notothyrial platform with deeply crenulated crests, like that of the median cardinal process itself (Pl. 2, fig. 20). In valves over 10 mm. long a variable degree of fusion occurred between these lateral ridges and the main median myophore so that the antero-ventral face of the cardinal process and notothyrial platform became trilobed with the notothyrium almost filled by the three myophore ridges (Text-fig. 4). Additional shell deposition antero-laterally on the median lobe may have resulted in it having become bifid and in its covering the two

lateral lobes. The adult cardinal process is, therefore, a composite trilobed structure, as reported by Demanet (1934 : 47), built principally of the median primary lobe, but accompanied by secondary lateral lobes added during growth.

In discussing the cardinal process of British Avonian *Schizophoria* George & Ponsford (1938 : 233) illustrate serial sections of several specimens and conclude that, while it is variable in form, the cardinal process commonly consists simply of a median serrated "node". Section 4c, of *S. nuda* George & Ponsford, would be like that of the Fermanagh specimens if the "accessory processes" flanked the median ridge rather than both being on one side. It is possible that less widely spaced sections would have revealed the secondary lateral lobes and the more ridge-like nature of the cardinal process across the notothyrial floor. A comparison of type material of *S. nuda*, preserved as internal moulds in the British Museum (Natural History) (BB.2407-2411), with brachial valve interiors reasonably assigned to *S. resupinata* s.s. (Pl. 2, figs. 5, 6) shows that the two are probably comparable within the limits of specific variation. Bond retained *S. nuda* principally because of its unusual state of preservation, but this hardly seems a worthy reason for specific distinction.

In her study of Mid-Devonian orthoids from Poland, Biernat (1959 : 57) describes and figures the variation to be seen in the cardinal process of adult *Schizophoria striatula* (Schlotheim). She writes that the cardinal process "may be single or bifid", although it would seem from her figures (1959, text-fig. 20, and pl. 9, figs. 1, 2) that the cardinal process of her material probably grew in a similar way to that of the Fermanagh specimens, viz. the variation being around a basically trilobed structure. The difference would seem to be one of terminology, for in her discussion of the ontogeny of the cardinal process, Biernat describes how "2 or 3 elevations appear in the notothyrial cavity on each side of the cardinal process" and continues by

TABLE I

\bar{l} mm. (var.) = 6.76 (14.613)	\bar{l} mm. (var.) = 6.76 (14.613)
\bar{w} mm. (var.) = 8.42 (22.280)	\bar{th} mm. (var.) = 2.01 (1.189)
r = 0.996	r = 0.990
a (var.) = 1.235 (0.00111)	a (var.) = 0.285 (0.00015)
\bar{x} mm. (var.) = 8.42 (22.280)	\bar{dl} mm. (var.) = 6.76 (14.613)
\bar{x} mm. (var.) = 4.79 (8.355)	\bar{di} mm. (var.) = 2.72 (2.838)
r = 0.987	r = 0.992
a (var.) = 0.612 (0.00089)	a (var.) = 0.441 (0.00028)
\bar{dl} mm. (var.) = 2.72 (2.838)	
\bar{di} mm. (var.) = 1.95 (0.866)	
r = 0.974	
a (var.) = 0.552 (0.00142)	

TABLE I. Statistics of length (\bar{l}), maximum width (\bar{w}), width of hingeline (\bar{x}), thickness (\bar{th}), and length (\bar{dl}) and width (\bar{di}) of the diductor muscle scars of 13 pedicle valves of *Schizophoria resupinata dorsosinuata* Demanet.

TABLE 2

No. of ribs.	12	13	14	15	16
No. of specimens	2	6	8	3	1

TABLE 2. The number of ribs counted in a width of 2.5 mm., 5 mm. antero-medially from the umbo of 20 pedicle valves of *Schizophoria resupinata dorsosinuata* Demanet.

TABLE 3

\bar{l} mm. (var.) = 5.14 (7.398)	\bar{l} mm. (var.) = 5.14 (7.398)
\bar{w} mm. (var.) = 6.42 (11.899)	\overline{th} mm. (var.) = 1.31 (0.441)
$r = 0.998$	$r = 0.926$
	a (var.) = 0.244 (0.00053)
$\log_e \bar{l}$ (var. $\log_e l$) = 1.514 (0.2469)	\bar{l} mm. (var.) = 5.14 (7.398)
$\log_e \bar{w}$ (var. $\log_e w$) = 1.552 (0.2791)	\overline{ad} mm. (var.) = 2.31 (1.446)
$r_e = 0.997$	$r = 0.987$
α (var.) = 1.063 (0.00045)	a (var.) = 0.442 (0.00034)
\bar{w} mm. (var.) = 6.42 (11.899)	\overline{ad} mm. (var.) = 2.31 (1.446)
\bar{x} mm. (var.) = 3.01 (2.714)	\bar{v} mm. (var.) = 2.18 (0.773)
$r = 0.998$	$r = 0.949$
a (var.) = 0.478 (0.00006)	a (var.) = 0.731 (0.00213)
\bar{s} mm. (var.) = 1.18 (0.206)	\bar{l} mm. (var.) = 5.14 (7.398)
\bar{t} mm. (var.) = 1.92 (0.503)	\bar{s} mm. (var.) = 1.18 (0.206)
$r = 0.963$	$r = 0.976$
a (var.) = 1.563 (0.0119)	a (var.) = 0.167 (0.00020)

TABLE 3. Statistics of length (l), maximum width (w), thickness (th), width of hinge-line (x), length of adductor scars (ad), width of adductor scars (v), length of the extent of the brachiophores (s) and the width at the brachiophore tips (t) of 17 brachial valves of *Schizophoria resupinata dorsosinuata* Demanet.

saying that the adult anterior aspect may be "multifid" while the lateral elevations became thicker and "together with the cardinal process fill all width of the notothyrial cavity". It seems, therefore, that she retains the term cardinal process only for the central "single or bifid" ridge within the notothyrial cavity and looks upon the lateral "elevations" as being separate structures. She does not indicate a function other than that of diductor muscle attachment, nor does she differentiate the "cardinal process" from lateral elevations in text-fig. 20 (1959: 57) and it would seem more reasonable to include all outgrowths of the notothyrial platform as constituents of the cardinal process. The intimacy and degree of fusion between the lateral ridges and the median ridge preclude the possibility that the lateral ridges bore the dorsal adjustor muscles.

The internal surfaces of the valves are variably thickened, specimens from Carrick Lough commonly being thinner than those from Bunnahone. In these thinner shelled specimens traces of the radial mantle canals are more prominent, being marked by low bordering ridges, and are represented externally by slightly accentuated radial ribs. A deepening of these canal traces is usually terminated anteriorly by a rib aperture (Pl. 2, fig. 37) which only retained a broad connection to the outer surface while still close to the valve margin. In some young thin-shelled forms up to 7 or 8 mm. long, the traces of each follicular embayment can be followed back to the muscle field, but more commonly secondary shell obscured these, except over the last 1 mm. towards the valve margin. All these traces probably mark the positions of small mantle canals that led to each setal follicle at the mantle edges.

Accentuated "growth-lines" tend to be more crowded anteriorly, indicating retradations of late growth, and it may be that these specimens were living in conditions marginal to their optimum habitat so never reaching a size more typical for the species.

Family **RHIPIDOMELLIDAE** Schuchert 1913

Genus **RHIPIDOMELLA** Oehlert 1890

TYPE SPECIES. *Terebratula michelini* L'Eveillé, by original designation of Oehlert (1890 : 39).

Rhipidomella michelini (L'Eveillé) 1835

(Pl. 3, figs. 1-25, Text-fig. 5)

DIAGNOSIS. Gently dorsibiconvex *Rhipidomella* with prominent, trifid cardinal process and well developed posteriorly convex chilidial plates; ventral diductor scars subrhomboidal in outline, about three-fifths valve length and without strong postero-laterally enclosing ridges.

DESCRIPTION. Outline subrounded to rounded trigonal, hinge-line about two-fifths maximum width which is anterior of mid-length, length slightly less than width, adult anterior margin only gently curved; profile biconvex with depth slightly less than one-half length; slight median sulcation of brachial valve and antero-median flattening of pedicale valve; multi-costellate with 9 or 10 ribs in 2.5 mm., 5 mm. antero-medianly from dorsal umbo, costellae added by bifurcation; growth-lines sporadic and prominent; ventral interarea concave, apsacline, dethyrium open with apical angle of about 80°; dorsal interarea shorter, orthocline to anacline, notothyrium more or less closed by chilidial plates; teeth strong, diverging antero-dorsally at about 40° from mid-line, dental plates vertically disposed but slightly divergent to valve floor; pedicle callist developed apically, dental plates with anteriorly directed notches to receive postero-ventral apophyses of brachiophores; adductor field small, oval to rectangular and anteriorly raised; diductor scars variably impressed, adult scars lobate to subflabellate, surrounding adductor scars, anteriorly ridged and surrounded by slight thickening from bases of dental plates; valve margins strongly crenulated; cardinal process prominent, distally trifid with

median ridge extending beyond lateral ridges, postero-laterally enclosed by chlidial plates from below which strong brachiophores extend at 35° to 40° from mid-line; inner faces of brachiophores curved, and bases recurved to floor of valve to enclose deep sockets; adductor field quadrate to trigonal, extending about one-half valve length and separated by low wide ridge which may accommodate dorsal adjustor muscle scars posteriorly, adductor scars possibly divided with more prominent rounded-quadrate anterior scars.

MEASUREMENTS (in mm.)

	length	width
Complete shell (BB.52718)	10.9	11.7
Pedicle valve (BB.52719)	8.8	—
Complete pedicle valve (BB.52720)	9.2	9.9
Incomplete pedicle valve (BB.52721)	—	c. 15.0
Complete brachial valve (BB.52722)	7.6	8.5
Brachial valve (BB.52723)	7.0	7.3
Complete shell (BB.52724)	4.6	5.0
Young pedicle valve (BB.52725)	3.4	3.6
Young brachial valve (BB.52726)	3.4	3.6

DISCUSSION. Unlike many species of *Rhipidomella*, which are dorsibiconvex, the present material is almost equibiconvex. While both valves are approximately equal in depth, the convexity of the pedicle valve is greatest posteriorly, close to the umbo, and that of the brachial valve near to its mid-length. These differences are associated with the anterior flattening of the pedicle valve and the median to antero-median slight sulcation of the brachial valve; features which led to a faintly bilobed body cavity. The form of the valve profile is also associated with the radial ornament. It can be demonstrated that there is a distinct tendency for branching of costae and costellae to occur downslope, i.e. over the medianly sulcate region of the brachial valve branching took place more commonly from the median sides ("internal" of Bancroft (1928 : 60)), whereas on the flanks, branches commonly arose laterally ("externally" Bancroft) (Williams & Wright 1963 : 22). The relationship between the mantle edge and the shell margins of dalmanellids has been discussed by Williams & Wright (1963 : 19), and it seems likely that the radial ornament of such shells is intimately associated with the mantle canal system. The grooves seen at certain growth stages on some of the follicular eminences, the shell protuberances between each setal follicle, can be related to external rib branchings. These grooves soon reached the dimensions of the previously formed follicular embayments and became buried in secondary shell deposits posteriorly, so that it is only rarely possible to see the positions of the branchings internally. However, externally they are commonly clear and probably accurately mark the positions of canal and follicular proliferations.

The follicular eminences and embayments form a prominent marginal crenulation in rhipidomellids. The use of these crenulations for supra-specific taxonomic discrimination raises difficulties. Crenulations vary in detail according to both the

age of the brachiopod and their distance from the margin of the shell. Certainly the Fermanagh specimens, believed to be conspecific with the type species of *Rhipidomella*, show variation in the cross-section of their crenulations (Text-fig. 5) at different distances from the margin. It is important, therefore, to define closely any such variation used as taxonomic criteria.

A comparison of a small collection of *R. henryhousesensis* Amsden, recently placed in *Dalejina* by Boucot *et al.* (1963 : 337), with the Fermanagh specimens shows that differences in their marginal crenulations exist, but other differences may be noted; the absence of chilidial plates and more equally branching ribs in the American species. These differences are, at the best, merely observations, as the American

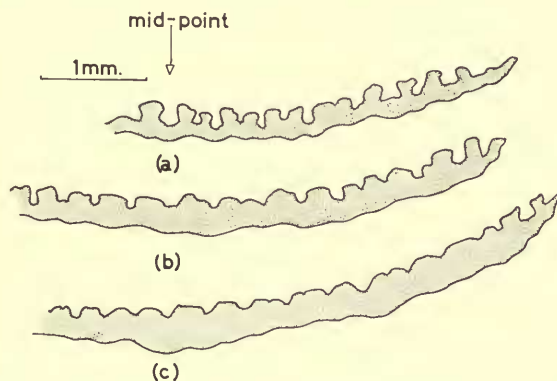


FIG. 5. Three transverse sections parallel to the hinge-line of *Rhipidomella michelini* (L'Eveille) showing the anterior internal marginal crenulations. The mid-point of the shell is indicated on the sections which are 0.4 mm., (a), 0.6 mm.; (b), and 0.8 mm.; (c) from the anterior edge of the shell.

material at hand appears to be slightly abraded. A more equal rib branching, i.e. one in which the branching approaches dichotomy, in *R. henryhousesensis* could explain the more regular grooves on the follicular eminences at the valve margins. This seems to be fairly persistent throughout ontogeny, whilst in the Fermanagh specimens a closely comparable style of branching was usually restricted to the first few mm. of growth.

The rib apertures (or hollow ribs) of *Rhipidomella* are well known and have been assumed to be the bases of spinose extensions of the shell (Davidson 1861 : 133, pl. 30, figs 6, 7). The frequency of these apertures is not constant in *R. michelini*, but is commonly 3 in 5 mm. length of rib. The apertures face anteriorly and away from the valve surface at a low angle, their openings being hooded by the rib posteriorly. Anteriorly the rib is suppressed for a short distance leaving a slight depression. At no time has any sign of spine-like prolongations been seen attached to the valves, either from the Fermanagh fauna or from specimens from Clattering Dykes, possibly figured by Davidson (1861, pl. 30, fig. 6). The openings lead posteriorly along the rib and into the shell substance at a narrow angle. However, only marginally do they open internally on to the floor of one of the follicular embayments. Because of the rapid infilling of these embayments by secondary

shell, the openings do not persist over the internal surfaces and, therefore, could not have contained living tissue unless connected by thin strands, such as those joining to the caecae. It is conceivable that the apertures were analogous to the hollow spines of productoids (also commonly marginal) in providing some sort of sensory receptors.

In all known aspects other than the prominence of the muscle scars, in particular the ventral diductor scars, the shells of the Fermanagh fauna agree with the type species *R. michelini* (L'Eveillé), as described by Demanet (1934 : 37, pl. 2). Although the longest valves reach about 12 mm. the muscle scars are all faintly impressed and it seems clear that differential shell deposition alone was responsible for the prominence of the scars found in larger specimens of *R. michelini*.

Campbell (1957 : 51) casts doubt upon the assumption that the dorsal adductor scars were divided into two pairs in the Lower Carboniferous species. Judging from the present material and topotypic material from Belgium (Pl. 3, fig. 5) his doubts seem valid, and no posterior scars have been distinguished with certainty. Demanet (1934 : 39), Dresser (1954 : 22), and Campbell (1957) believe the pedicle callist (Schuchert & Cooper 1932 : 9) to be the seat of the ventral pedicle adjustor muscles. However, it is more likely that it developed because of the anterior retreat of the junction between the pedicle and outer epithelium (Williams 1956 : 255, who termed it the "pedicle collar"). The umbonal cavity, between the dental plates, probably accommodated the base of the pedicle, to which were attached adjustor muscles extending antero-laterally across the cavity floor onto the bases of the dental plates. The dorsal adjustor muscles probably passed between and anterior to the dorsal ends of the diductor muscles and were attached posteriorly between the dorso-medial bases of the brachiophores, close to the base of the cardinal process.

TABLE 4

\bar{l} mm. (var.) = 4.69 (8.340)	\bar{l} mm. (var.) = 4.69 (8.340)
\bar{w} mm. (var.) = 5.01 (8.836)	\bar{x} mm. (var.) = 2.34 (1.709)
$r = 0.997$	$r = 0.995$
a (var.) = 1.029 (0.000213)	a (var.) = 0.452 (0.00014)
\bar{w} mm. (var.) = 5.01 (8.836)	\bar{x} mm. (var.) = 2.34 (1.709)
\bar{b}_2 mm. (var.) = 1.64 (0.523)	\bar{y} mm. (var.) = 2.20 (1.488)
$r = 0.941$	$r = 0.992$
a (var.) = 0.245 (0.00045)	a (var.) = 0.936 (0.00046)
\bar{b}_1 mm. (var.) = 0.74 (0.138)	
\bar{b}_2 mm. (var.) = 1.64 (0.523)	
$r = 0.939$	
a (var.) = 1.947 (0.0298)	

TABLE 4. Statistics of length (l), maximum width (w), length to which the adductor scar extends (x), width of adductor scars (y), and the widths of the brachiophores at their junctions to the interarea (b_1) and at their anterior tips (b_2) in 17 brachial valves of *Rhipidomella michelini* (L'Eveillé).

TABLE 5

Delthyrial angle	65°	70°	75°	80°	85°
No. of specimens	1	3	3	8	2

TABLE 5. The total angle of divergence of the teeth and margins of the delthyrium, in 17 pedicle valves of *Rhipidomella michelini* (L'Eveillé).

TABLE 6

\bar{l} mm. (var.) = 4.39 (6.200)	\bar{l} mm. (var.) = 4.39 (6.200)
\bar{w} mm. (var.) = 4.70 (6.859)	\bar{th} mm. (var.) = 2.06 (0.915)
$r = 0.995$	$r = 0.989$
a (var.) = 1.052 (0.00031)	a (var.) = 0.384 (0.00009)

TABLE 6. Statistics of length (l), width (w), and thickness (th) of 20 shells of *Rhipidomella michelini* (L'Eveillé).

TABLE 7

No. of ribs	8	9	10
No. of specimens	4	7	6

TABLE 7. The number of ribs in a width of 2.5 mm., 5 mm. antero-medially of either umbo on *Rhipidomella michelini* (L'Eveillé).

Order STROPHOMENIDA Öpik 1934

Superfamily STROPHOMENACEA King 1846

Family LEPTAENIDAE Hall & Clarke 1894

nom transl. Cooper 1956

Subfamily LEPTAENINAE Hall & Clarke 1894

Genus LEPTAGONIA M'Coy 1844

- 1844 *Leptagonia* M'Coy: 116 (pars).
 1846 *Leptaena* King: 28 (pars).
 1852 *Leptaena* (*Leptagonia*) M'Coy: 223 (pars).
 1861 *Strophomena* Davidson: 119 (pars).
 1929 *Leptagonia* Schuchert & LeVene: 74.
 1947 *Pseudoleptaena* Miloradovich: 96.
 1952 *Leptaenella* Sokolskaja: 35, *non Leptaenella* Fredericks 1917.
 1958 *Leptagonia* M'Coy; Cvancara: 859.

DIAGNOSIS. (emended) Biconvex, strongly geniculate and rugose Leptaenidea; ventral and dorsal muscle scars situated upon prominent pseudospondylium and complex muscle platforms respectively.

DESCRIPTION. Outline irregularly quadrate, profile of adult disc biconvex, dorsally directed trail variably developed, commonly affected by opposite folding; rugae regularly and concentrically developed on disc; costae fine, even, rarely branching dichotomously; ventral interarea apsacline, delthyrium wide, covered apically by pseudodeltidium in various stages of resorption, foramen supra-apical, commonly sealed in adult shells; dorsal interarea short anacline, chilidium large; teeth strong, widely divergent, crenulated; dental lamellae continuous with subcircular pseudospondylium, elevated anteriorly; lanceolate adductor scars on broad median ridge; antero-lateral areas of ventral disc rarely raised as low mounds; cardinal process lobes strongly projecting from beneath chilidium with posteriorly directed myophores and strongly curved bases defining subcircular hollow; dorsal adductor field borne on complex platform with elevated subquadrate posterior scars, highly arched in young valves, flanking raised triangular to rectangular anterior scars separated posteriorly by low ridge of secondary shell and anteriorly by deep groove from which median septum extends anteriorly; adult disc enclosed anteriorly by secondary ridge; mantle canal system pinnate to lemniscate; shell substance pseudopunctate.

TYPE SPECIES. *Producta analoga* Phillips by subsequent designation of Schuchert & LeVene (1929 : 74).

DISCUSSION. The genus *Leptaenia* was originally established by M'Coy in 1844, and was later defined by him as including shells with "both valves abruptly bent at right angles towards the entering" (brachial) "valve and the rostral portion concentrically wrinkled" (1852 : 233). This was done in the belief that *Leptaena* Dalman was typified by *Leptaena transversalis* Dalman (now *Plectodonta transversalis*, and thereby restricted to plectambonitacean-like shells).

Six species were described by M'Coy and assigned to *Leptaenia*, the first being *Producta analoga* Phillips, a poorly defined species from the Lower Carboniferous of Bolland, Yorkshire, and Redesdale, Northumberland, but at that time believed to be closely related to *Leptaena depressa* J. de C. Sowerby and *L. rugosa* Dalman from the Upper Silurian and Upper Ordovician respectively, and also to *Productus plicatilis* J. de C. Sowerby (now type species of *Plicatifera* Chao. from the Carboniferous). In 1855 he included *Leptaena distorta* J. de C. Sowerby within *Leptaenia*, a species also from the Lower Carboniferous.

Davidson (1861 : 119-122) concluded that *L. depressa*, *L. analoga* and *L. distorta* were synonymous and did not merit more than varietal rank of *Strophomena rhomboidalis* (Wahleberg).

In describing *Leptaena* as a species of *Strophomena*, Davidson was exercising the conservatism that pervaded his approach to brachiopod systematics, because King (1846) had already named a rugate, geniculate species of Dalman, viz. *Leptaena rugosa* (see Spjeldnaes 1957 : 172) as type species of *Leptaena*.

Until recently most palaeontologists have accepted the Carboniferous form as a true *Leptaena*, differing only specifically from *L. rugosa*, *L. rhomboidalis*, *L. depressa*, etc. although Hall & Clarke (1891 : 280) did observe that "the extreme differentiation of the muscular area as described is even more distinctly exhibited in the forms

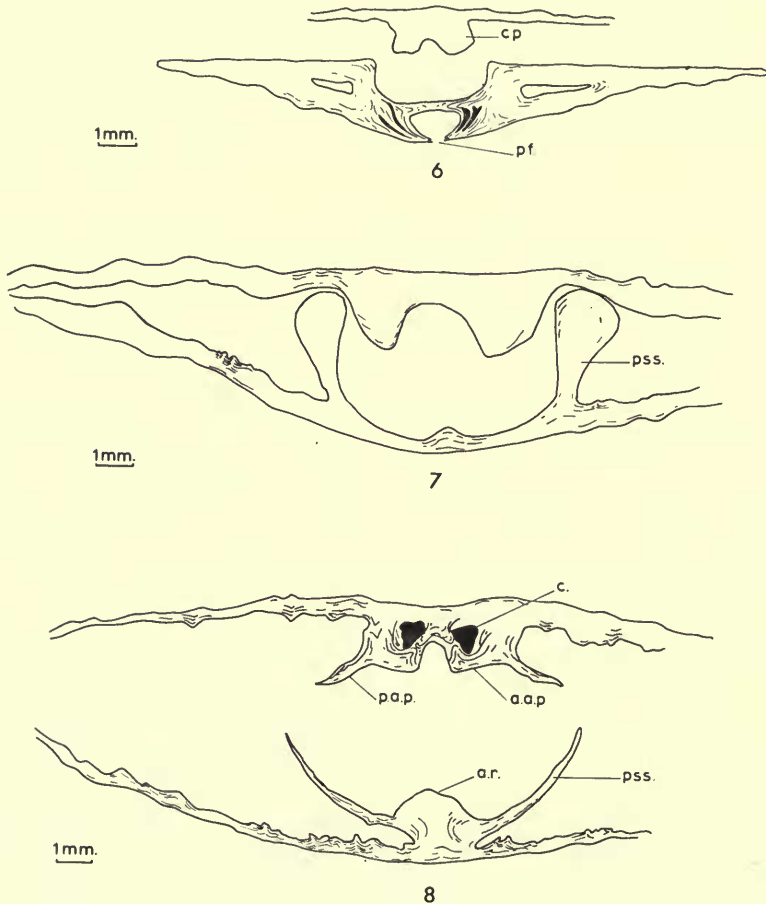
of the early Carboniferous than in those of the Silurian and Devonian". During the early part of this century *L. analoga* continued to be thought of as a true *Leptaena*; admittedly Schuchert & LeVene (1929) designated the species as the type of *Leptagonia*, but then promptly described M'Coy's genus as a subjective synonym of *Leptaena*.

In 1947, Miloradovich proposed the genus *Pseudoleptaena* for leptaenids with a pseudospondylium and a cruralium and cited *L. distorta* Sowerby as the type; and in 1952 Sokolskaja erected the genus *Leptaenella* for leptaenids with a ventral pseudospondylium, naming *P. analoga* Phillips as type species. In so doing she was evidently unaware that not only had *P. analoga* been already designated as the type species of *Leptagonia* by Schuchert & LeVene, but also that *Leptaenella* had already been proposed by Fredericks (1918 : 89) for certain Devonian leptaenids that appear to be congeneric with *Leptaena* s.s. Thus, in effect, Russian palaeontologists are recognising the generic validity of *Leptagonia* and the problem becomes one of deciding firstly, if *Leptagonia* is sufficiently distinct from *Leptaena* to warrant resuscitation; and secondly whether *Pseudoleptaena*, as typified by *L. distorta*, is also different enough to be retained.

Some of the more pertinent features that differentiate *Leptagonia* from *Leptaena* are as follows. In *Leptaena* geniculation is like an exaggeration of the anterior ruga so that both valves bend in the same direction, whereas *Leptagonia* is dominantly biconvex as a result of valve growth towards the commissural plane, prior to the strong geniculation. Although the ventral interiors do not greatly differ in general arrangement, the pseudospondylium of *Leptagonia* is an expression of anterior growth of the confining rim of the ventral muscle field away from the floor of the valve and as such is developed more fully than in *Leptaena* (Pl. 3, fig. 28; Text-fig. 7). Anteriorly it is so elevated as to simulate a true spondylium simplex (Text-fig. 8). The superficial pattern of the dorsal muscle fields for *L. depressa* and *Leptagonia* are similar, but it originates in different ways. In *Leptaena* the dorsal adductors were attached directly to the floor of the brachial valve and were surrounded or slightly elevated by normal processes of shell accretion during growth of the shell. The ontogenetic development of the dorsal muscle field of *Leptagonia*, as seen in a series of dorsal interiors varying in width from 3.7 mm. to 60 mm., on the other hand, was intimately connected with two pairs of muscle plates. In the smallest specimens these plates arise from the floor of the valve, a median pair from below the cardinal process extending anteriorly and separated by a deep groove; and a lateral pair arising from the anterior edges of the socket plates and extending anterolaterally to flank the median pair. These plates are only fused to the floor of the valve posteriorly and at their lateral margins (Text-fig. 10) so as to form anteriorly and antero-laterally directed cavities, all of which must have contained folds of the dorsal mantle epithelium during early life. Each pair of plates respectively accommodated the bases of the anterior and posterior adductor muscles. At the same stage of growth, a pair of ridges extended anteriorly from the points of coalescence of the posterior and anterior adductor plates with each other and with the floor of the valve, which continue parallel to the median septum, at a distance of 0.7 mm. on either side of it and for approximately one-half of its length (Pl. 4, fig. 7); they are thought to have defined

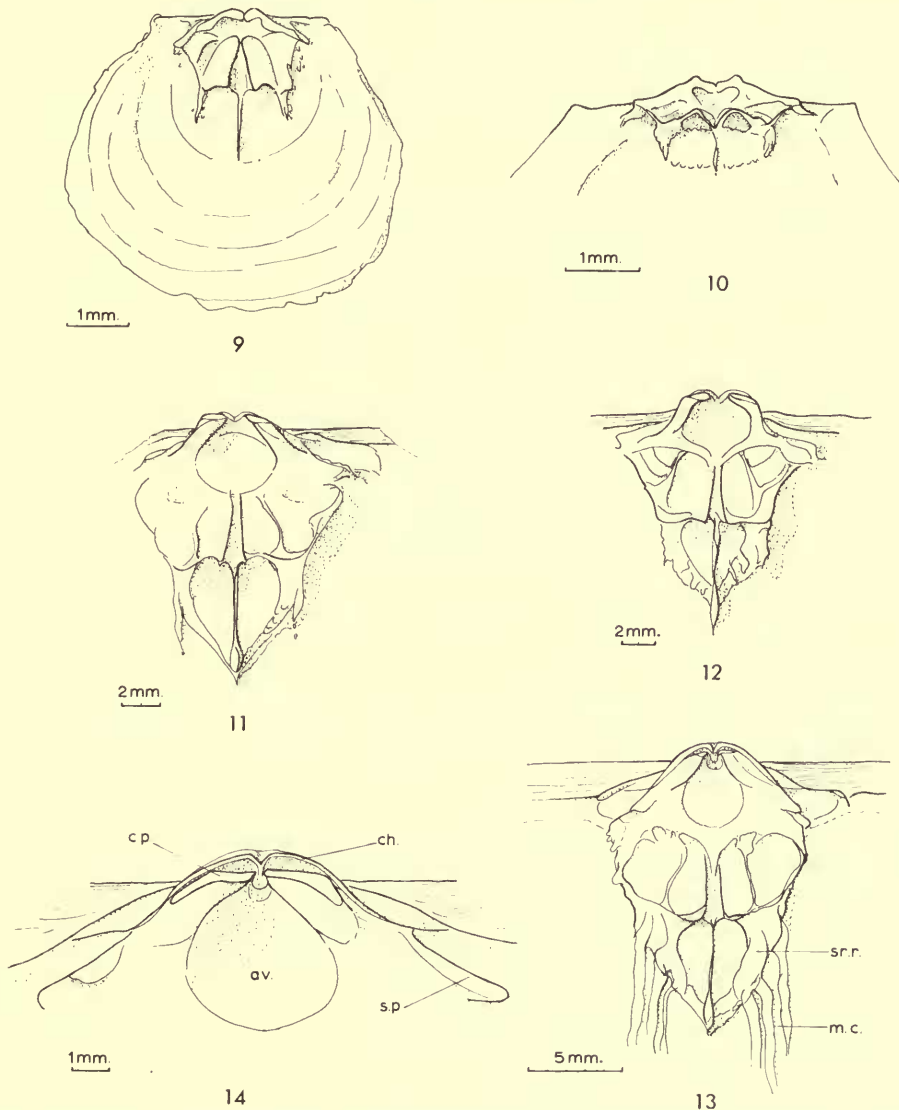
the *vascula myaria* which probably continued posteriorly along the depression between the anterior and posterior adductor plates. It is also possible that the body wall, separating the visceral and brachial cavities, may have been supported at these ridges.

In brachial valves with the median septum extending anteriorly for a distance of about 9 mm., a considerable amount of shell thickening has taken place. The lobes of the cardinal process had grown ventrally and are separated distally by a notch of variable dimension, containing the median indentation of the chilidium. The rounded pit below the cardinal process is encased in secondary shell obliterating the posterior ends of the adductor plates. (Text-fig. 11). These progressively lost



FIGS. 6-8. Illustrations of transverse sections of *Leptagonia analoga* (Phillips) at 2.0 mm., Fig. 6; 3.0 mm., Fig. 7; and 4.5 mm., Fig. 8. from the ventral umbo of a specimen about 30 mm. wide across the visceral disc. *a.a.p.*, anterior adductor platform; *a.r.*, adductor ridge in pedicle valve; *c.*, cavity below dorsal adductor platform; *c.p.*, cardinal process; *p.a.p.*, posterior adductor platform; *p.f.*, pedicle foramen; *pss*, pseudospondylium.

their tent-like shape through infilling of the underlying chambers; presumably during the anterior withdrawal of the mantle epithelium and through secondary shell deposition by the epithelium associated with the muscle bases. Concurrently, the ridges lateral to the median septum became increasingly prominent and thickening



FIGS. 9-14. Illustrations of the ontogeny of the brachial valve interior of *Leptagonia analoga* (Phillips) (Figs. 9-13), and details of the adult cardinal process (Fig. 14). All viewed dorsally except fig. 10, viewed postero-dorsally. *av*, "alveolus", the subcircular hollow between the bases of the cardinal process; *ch*, chilidium; *c.p.*, cardinal process; *m.c.*, traces of the mantle canals; *s.p.*, socket plates; *sr.r.*, ridge surrounding the sub-rhomboidal region.

occurred between them and the anterior part of the median septum to produce a subrhomboidal structure enclosing the septum anterior to the adductor plates (cf. *Leptaena rhomboidalis*). From the lateral corners of this area small subsidiary ridges extend forward which probably defined the outer edges of the *vascula myaria* trunks. At this stage, the lateral and anterior borders of the adductor plates remain discrete from the valve floor, but the degree of arching seldom exceeds 1 mm. In specimens whose median septum extends 11 mm. from the base of the cardinal process, the posterior adductor plates are generally raised above those associated with the anterior adductor scars (Text-fig. 12). However, this is a temporary feature, as large specimens, with a median septum of 16.5 mm. have both adductor scars at much the same level.

In the largest specimens, the infilling of the chambers below the adductor plates is almost complete, only the lateral margins of the posterior plates showing slight arching. The anterior and posterior scars are less well differentiated, only being separated by a low ridge (Text-fig. 13). The posterior and median borders of the muscle fields are well defined by the continued deposition of secondary shell so as to form a short median ridge extending from the pit between the cardinal process lobes and terminating in the groove between the anterior scars. The subrhomboidal area is well developed and the shell especially thickened round the anterior region of the median septum. The small subsidiary ridges, marking the *vascula myaria* can now be traced anteriorly to where they branch towards the anterior margin of the brachial cavity. By this stage the cardinal process lobes are well separated ventrally and their flat ends are slightly striated for the reception of the dorsal diductor bases. The chilidium had grown ventrally to enclose the posterior faces of the lobes in such a way as to form two cavities from which the diductor muscles extended (Text-fig. 14).

The point of articulation of the valves was always anterior to the interareas, so that during growth the chilidium extended antero-laterally to infill the redundant posterior regions of the sockets. This complicated development contrasts strongly with the simple accretionary processes that were responsible for the differentiation of the dorsal adductor scars of *Leptaena*.

From a provisional investigation of Devonian *Leptaena* in collections from Germany and North America it would seem that internal morphology is intermediate between Silurian *Leptaena* and Carboniferous *Leptagonia*. The Devonian muscle fields are more elevated, especially anteriorly, than those of Silurian specimens, and the cardinal process, with its supporting ridges is comparable to *Leptagonia* in that the myophore bases diverge antero-ventrally to enclose a deep rounded alveolus. The socket ridges are characteristic in *Leptagonia* as they curve smoothly onto the cardinal process rather than being sharply distinct as in *L. depressa* and *L. rhomboidalis*.

In his original description of *L. distorta*, the type species of *Pseudoleptaena*, J. de C. Sowerby (1840 : 10) referred to it as having "A thicker shell than *L. analoga*; well distinguished by its projecting beak, very convex valves, which are not compressed near the beak, and its smaller size." The specimens were collected by Gilbertson from the Isle of Man. This description would be adequate for shells at a

stage of development as illustrated in Text-figs. 11 and 12, which are essentially the same as text-fig. 27 of *Pseudoleptaena distorta* in Sarycheva & Sokolskaja (1952 : 37). Thus, the cruralium and pseudospondylium of Miloradovich's genus are developmental stages in the growth of the adult *Leptagonia* and invalidate the retention of *Pseudoleptaena* as a distinct genus.

The mantle canal system of *Leptagonia* differs somewhat from that illustrated for *Leptaena* by Williams (1956 : 274). His illustration shows saccate gonocoels surrounded by major sinus trunks from which are given off numerous peripheral sinuses. In *Leptagonia* it appears that the gonocoels themselves were lemniscate, giving off the peripheral sinuses (Pl. 3, fig. 30), with the *vascula media* and *myaria* retained medianly (Text-fig. 15). However, it might be that this condition is only apparent, and could have developed from the pattern illustrated by Williams by the enlargement of the gonocoels so as to have ruptured some of the more peripheral mantle sinuses and their main connecting trunks. Fragments of traces of the mantle

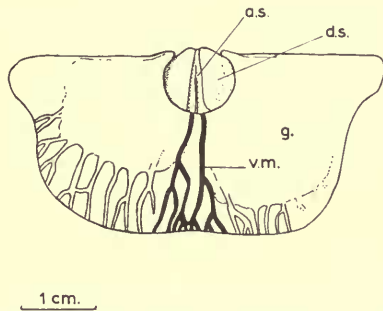


FIG. 15. Illustration of an internal mould of the pedicle valve of *Leptagonia analoga* (Phillips), showing the impressions of the pseudospondylium and mantle canals; *a.s.*, scars of adductor muscles; *d.s.*, scar of diductor muscles; *g.*, gonocoel, with traces of peripheral canals; *v.m.*, *vasculum medium* canal traces.

canals can be seen throughout most of the thickness of the shell substance and always seem to arise from the edges of the gonocoel, rather than from main *vascula* trunks, so that it seems unlikely that overgrowth of the gonadial regions has obliterated a former pattern of the mantle canal system. Cvancara (1958 : 861) speaks of "two suboval areas" on either side of the dorsal and ventral muscle fields which he says "appear" to be the only areas of pseudopunctation in *Leptagonia*. It seems likely that the regions to which he refers are the finely papillose areas, here considered as gonocoels (Pl. 4, fig. 2) and that he is incorrect in thinking the teleolae to be confined to those regions. Admittedly, there is a concentration of taleolae in the shell substance antero-lateral of the muscle fields, but they also occur within the shell substance of the muscle platforms and are scattered throughout the rest of the shell. From internal moulds it seems probable that the taleolae were also concentrated more strongly at the base of the trail. The pseudopunctae of *Leptagonia* are inwardly directed flexures of the shell fibres surrounding narrow non-fibrous taleolae so as to produce a closely fitting series of sharp cones, marked internally

by small tubercles. They were probably formed at the points of attachment of small muscle strands within the mantle, which may have assisted in the circulation or expulsion of the gonadial products from the mantle canal system, and in the movement of the mantle edges. Such an interpretation might explain the concentration of taleolae in the gonadial regions, and at the base of the trail.

An unusual feature seen rarely in pedicle valves is the development of two slight conical thickenings of the shell symmetrically placed between the pseudospondylium and the anterior margin of the disc. Similar, though more papillose humps are to be seen in some Silurian leptaenids, and may indicate that the spirolophe was slightly conical and directed towards the dorsal valve.

Longitudinal sections of young shells, of hinge-width approximately 2.5 cm. show an open supra-apical pedicle foramen. A study of the shell texture shows the canal through the shell to be lined with fibres disposed parallel to the canal surface and more or less normal to the ventral, external, surface of the valve, an area which

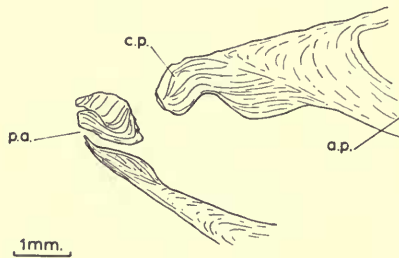


FIG. 16. Illustration of a median longitudinal section through a young shell of *Leptagonia analoga* (Phillips) showing the cavity below the dorsal adductor platform, thickening anterior to the cardinal process and the pedicle aperture with its lining of secondary fibrous calcite; *a.p.*, adductor platform; *c.p.*, cardinal process; *p.a.*, pedicle aperture.

must have been covered by chitin (Text-fig. 16). In describing his Australian specimens of cf. *L. analoga* Cvancara (1958 : 860) apparently noted the same feature for he states that "The foramen appears to be lined with a tubular sheath". The disposition of these fibres and their inferred relationship to the epithelium which secreted them is obscure, but it would seem likely that they were deposited during the withdrawal of the outer epithelium following the development and redundancy of the nepionic pedicle sheath (Arber 1939 : 84). Outer epithelium must have extended through the nepionic shell to have formed the pedicle sheath. During subsequent growth the withdrawal of the outer epithelium resulted in the deposition of fibres parallel to the pedicle canal and also drew its junction with the pedicle epithelium inwards, so lining the canal with chitin. Spaces within the shell substance, parallel to these fibres, suggest that there might have been periodic advance and retraction of the outer epithelium to pedicle epithelium boundary.

In 1958 Cvancara came to the same conclusions about the reintroduction of *Leptagonia* as the correct generic name for the distinctive Carboniferous leptaenids. He bases his reasoning upon a study of the ventral valves in which he observed the muscle field to be supported upon a "well-developed spondylium", in contrast to

the flat muscle field of *Leptaena*. Cvancara did not examine the type specimen of *L. analoga*, but there can be little doubt that the upper Tournasian specimens from New South Wales which he describes are closely comparable with Phillips' species.

Leptagonia analoga (Phillips)

(Pl. 3, figs. 26-31. Pl. 4, figs. 1-9. Text-figs. 6-17)

- 1836 *Producta analoga* Phillips: 116, pl. 7, fig. 10.
 1844 *Leptagonia analoga* (Phillips) M'Coy: 117.
 1861 *Strophomena rhomboidalis* var. *analoga* (Phillips) Davidson: 119, pl. 28, figs. 1-6, 9-13.
 1958 *Leptagonia* cf. *L. analoga* (Phillips); Cvancara: 860, pl. 100, figs 6-13.

DIAGNOSIS. Subquadrate to semicircular *Leptagonia* with adult disc about one-half as long as wide, outline commonly modified by emargination medianly and less commonly laterally; immature shells plano-convex, adult shells biconvex, about one-half as deep as long, commonly uniplicate, rarely parasulcate; dorsally directed trail variably developed; visceral region with 14-18 regular rugae having mean wavelengths of 1.0 mm. and 1.4 mm. for the fifth and tenth rugae; rounded costae, commonly 5 or 6 in 2 mm., 10 mm. antero-medianly of umbones; pseudospondylium subcircular, seven-tenths as long as wide and about one-third as long as length of disc; dorsal muscle field one-half as long as wide. median septum extending forward for about two-fifths length of disc.

MEASUREMENTS (in mm.)

	length	width
LECTOTYPE. Complete eroded specimen (B.8963)	c. 20	c. 44
Incomplete pedicle valve (L.3817/1)	32	c. 50
Incomplete brachial valve (BB.52731)	—	c. 54
Complete brachial valve (BB.52730)	6.0	c. 6.9
Internal mould (BB.55777)	30	c. 45
Complete shell (BB.52729)	c. 5.0	5.5

LOCALITIES AND HORIZONS: Lectotype from Bolland, Yorkshire. B.8936 (Pl. 3, figs. 26, 27).

L.3817/1 from the Caldwell Collection, Hunterian Museum, Glasgow, collected from the Lower Carboniferous of Carrick-on-Shannon, Counties Leitrim and Roscommon, Ireland.

BB.55777 Gilbertson Collection, probably from the Lower Carboniferous of the Isle of Man.

BB.52729-30. The subreefal limestones and shales of Bunnahone, 2 miles N.W. of Derrygonnelly, Co. Fermanagh. Low. D. zone.

B..52731. The Ballyshannon limestone of Streadagh Point, Co. Sligo, Ireland S₂.

DISCUSSION. There is considerable variation of outline and in the length of visceral disc at which geniculation took place, so that the number of rugae on the

ventral discs of nineteen specimens from Carrick-on-Shannon ranges from 13 to 23. The wave-lengths of the fifth and tenth rugae from the umbo varies from 0.8 mm. to 1.1 mm. (mean 1.0 mm.) and from 1.1 mm. to 1.6 mm. (mean 1.4 mm.), on 15 specimens. Costation was little affected by the point at which geniculation occurred and remains with 3, 6, 4 and 3 specimens having respectively 4, 5, 6 and 7 costae per 2 mm. width at 10 mm. antero-medianly from the ventral umbo. Almost invariably

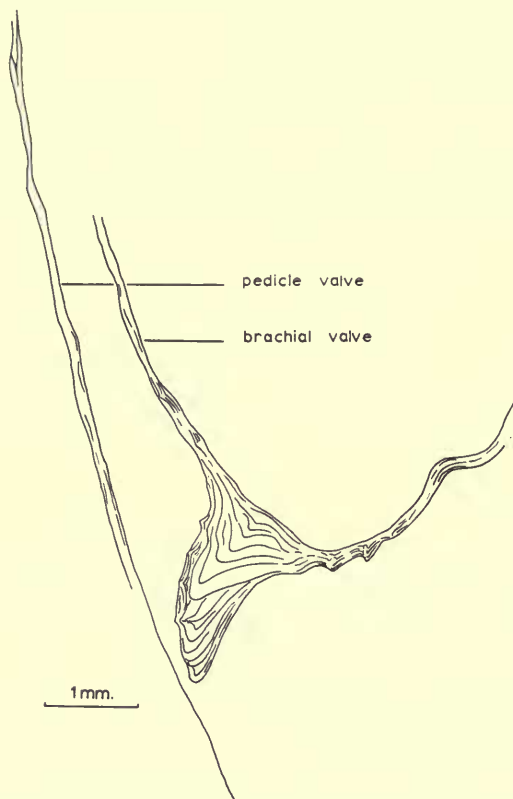


FIG. 17. Illustration of the anterior region of a median longitudinal section through the shell of *Leptagonia analoga* (Phillips) showing the secondary marginal ridge around the visceral region of the brachial valve, developed at the point of geniculation. The brachial cavity is to the right on the illustration.

the trail is depressed medianly, commonly also affecting the anterior margin of the disc to form a uniplicate commissure. Those shells which geniculated before the more usual disc length of about 27 mm. may be slightly depressed laterally as well as antero-medianly (cf. Davidson 1861, pl. 28, fig. 7). Such shells have been separated as *L. distorta*, but within large samples no satisfactory separation from *L. analoga* can be established. All contain the same internal structures at various stages of development, and the length at which the trail developed ranges from typical *L. distorta*, about 15 mm. long, to full sized specimens of *L. analoga*. It is necessary

to discover whether valid stratigraphic or facies differences occur within these forms before being at all sure of their taxonomic positions.

Irregularly concentric fine growth lines are continued on the trail, while the traces of the mantle canal system can also commonly be seen within the shell substance below every second or third rib. The rugae are not continued on to the trail.

The ridge around the adult dorsal visceral disc is of secondary shell material and becomes increasingly prominent through adulthood. (Text-fig. 17).

Only a few specimens of *L. analoga* were found among the etched material from Co. Fermanagh, but the author has made use of specimens in the Caldwell Collection from Carrick-on-Shannon, about 36 miles S.S.W. of Derrygonnelly, kindly lent by the Hunterian Museum, Glasgow. Measurements on 10 brachial valve interiors from this collection shows that the length of the median septum, measured from the posterior margin of the adductor field, is consistently similar to the total width of the socket ridges ($r = 0.924$).

Superfamily **DAVIDSONIACEA** King 1850

Family **ORTHOTETIDAE** Waagen 1884

Subfamily **ORTHOTETINAE** Waagen 1884

[= Derbyoidinae Thomas 1958]

Genus **BROCHOCARINA** nov.

1855 *Leptaena (Strophomena)* M'Coy: 450 (pars).

1861 *Streptorhynchus* King 1850: Davidson: 123 (pars) pl. 26, figs. 5 (?2 and 6) *non* Figs. 1, 3 and 4.

1910 *Schuchertella* Girty 1904; Thomas: 126.

1930 *Schuchertella* Smyth: 555, pl. 15, figs. 5-9.

DIAGNOSIS. Thin plano-convex Orthotitinae with entire chilidium; dental ridges deep, fusing posteriorly in ventral apex with trifold ridges enclosing lanceolate adductor scars.

DESCRIPTION. Outline subsemicircular, profile more or less plano-convex with narrow body cavity; ventral interarea long, apsacline, with arched pseudodeltidium, perideltidium variably defined; dorsal interarea and chilidium reduced; radial ornament parvicostellate with costellae regularly intercalated; teeth strong, continued at delthyrial margins as obliquely disposed posteriorly prominent dental ridges; ventral muscle field defined only in adult shells, adductor scars lanceolate, inserted posteriorly between low trifold ridges, diductor scars flanking and spreading anteriorly; cardinal process low, lobes well separated by sulcus with median chilidial ridge; socket plates at about 20° to hinge-line, slightly recurved; adductor field obscurely impressed, apparently flabellate to subcircular and separated by slight median ridge in adult shells; shell substance irregularly pseudopunctate.

TYPE SPECIES. *Schuchertella wexfordensis* Smyth 1930.

DISCUSSION. The new genus *Brochocarina* conforms to the requirements of the family Orthotetidae Waagen 1884, in having a low cardinal process and ventral

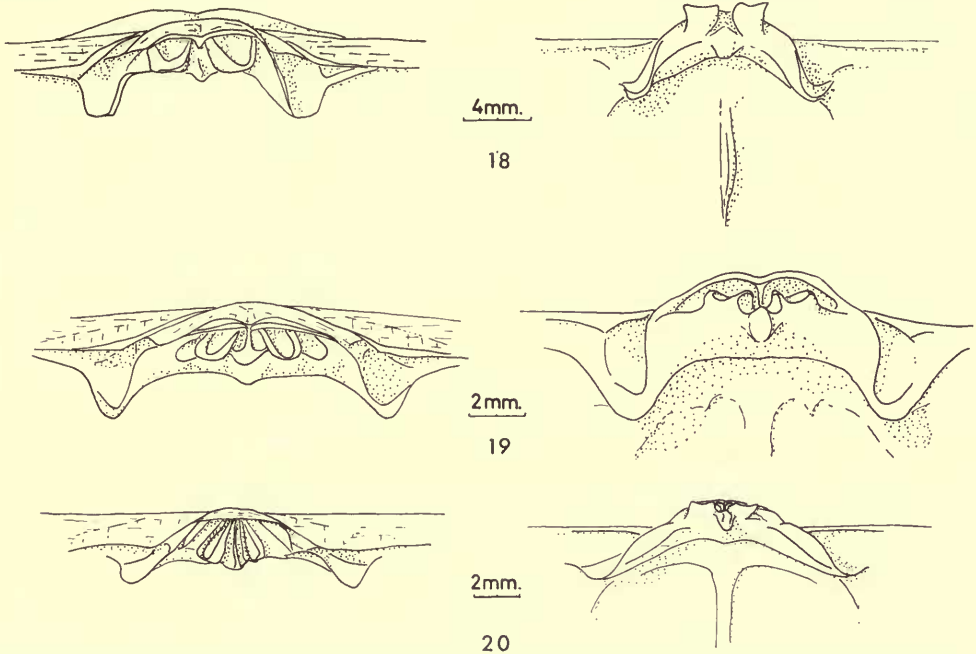
interior with a low median septum continuous with the inside of the pseudodeltidium and fused to the dental ridges. At subfamilial level the distinction between Orthotetinae Waagen, and Derbyiinae Stehli, is based upon the form of the socket plates; those genera with widely divergent socket plates, which tend to recurve towards the posterior margin as they fuse to the dorsal valve floor, being placed in the Orthotetinae, while those genera with less widely divergent socket plates, fusing to the floor without curvature, being assigned to the Derbyiinae. The genus possesses somewhat recurved socket plates, an ill-defined dorsal adductor field, greatly reduced dorsal interarea and small chilidium and is therefore assigned to the Orthotetinae.

The genera comprising the Orthotetinae are distinguished by differences in their ventral interiors, the form of the cardinal process lobes and the shell profile. *Brochocarina* differs from *Orthotetes* Fischer de Waldheim (? *Werriea* Campbell 1957) in having a less highly developed ventral median septum which has never been observed to have fused with the dental ridges posteriorly to such an extent as to have formed a delthyrial chamber (The "spondylium" of early authors and "secondary spondylium" of Thomas 1958 : 9). *Hipparionyx* Vanuxem is clearly distinguished by its subcircular outline, strongly impressed ventral interior and high, strongly divergent cardinal process lobes.

A comparison of the original descriptions of *Derbyoides* Dunbar & Condra (1932 : 114) and *Tapajotia* Dresser (1954 : 33) suggests that these genera are less distinctive than was thought by Thomas (1958 : 21) or by Dresser himself. While admitting "that *Tapajotia* is closely related to *Derbyoides*" Dresser separates the two largely on his mistaken belief that *Derbyoides* possesses a strong ventral median septum. In fact Dunbar & Condra (1932 : 115) state that "A median septum is present but rather weak and low, extending not over one-third the distance to the front of the valve", and inspection of their pl. 9, fig. 13 confirms this statement. For the above reasons Campbell (1957 : 46) states that *Tapajotia* "is probably a synonym of *Derbyoides*". This conclusion was arrived at by Mendes (1958 : 317, 319) in his review of the Tapajos River fauna of the Amazon Valley, and is supported by Cooper (personal communication). However, having studied topotypic material of *Derbyoides* and *Tapajotia* the writer is of the opinion that the two genera are distinctive and worthy of separation from *Brochocarina* gen. nov., while all three were probably closely related and derived from a schuchertellid stock.

The distinction between *Derbyoides* (Pl. 4, figs. 10-14) and *Tapajotia* (Pl. 4, figs. 15-23) include the following features. The brachial valve of *Derbyoides* is "strongly and rather evenly convex, with the highest point near the mid-length", (Dunbar & Condra 1932 : 115) and the valves are commonly faintly medianly sulcate in contrast to the plane, posteriorly flattened valves of both *Tapajotia* and *Brochocarina*. Dresser is mistaken in describing the widest part of *Tapajotia* as being "anterior" to the transverse mid-line. His illustrations, and the material at hand, show the greatest width to be at one-third the shell length, and the hinge-line width to be nine-tenths of this width. The greatest width of *Derbyoides* is at mid-length and the hinge-line is only three-quarters this width. The dorsal interiors differ in that a short median septum is developed between and anterior to the clearly impressed

adductor scars of *Derbyoides*, neither of which are seen in *Tapajotia*, and its cardinalia are more massive, extending for one-third of the hinge-line width as compared to one-quarter the width in *Tapajotia*. The ventral adductor scars are similar, but differ in being more elongately lozenge-shaped in *Derbyoides*, those of *Tapajotia* having more or less parallel lateral margins bordered by slight ridges. The delthyrial angle is about 20° greater in *Derbyoides* than in *Tapajotia* or *Brochocarina*, and its shell substance is much thicker and led to the development of marginal ridges around the edges of both valves.



FIGS. 18-20. Illustrations comparing the cardinalia of *Derbyoides* Dunbar & Condra (Fig. 18), *Tapajotia* Dresser (Fig. 19), and *Brochocarina* gen. n. (Fig. 20) in posterior (on the left) and internal (on the right) views.

Brochocarina is distinguished from both *Derbyoides* and *Tapajotia* primarily by reason of its ventral interior. The teeth of the American genera are traced along the edges of the delthyrium as low ridges which do not fuse at the beak of the valve to form a ventral median septum. The teeth of *Brochocarina* are supported by distinct dental ridges, strongly differentiated from the inner surface of the interarea. In adulthood these ridges reached almost to the valve floor and throughout life they fused posteriorly and gave rise to the tripartite median septum that separated and enclosed the lanceolate adductor scars (pl. 5, figs. 8, 13).

The dorsal cardinalia is similar to that of *Tapajotia*, but differs in that the socket plates diverge at 20° to 25° from the hinge-line instead of at about 35° in the Brazilian and Nebraskan genera (Text-figs. 18-20). The outline of *Brochocarina* tends to be more semicircular than that of the other genera, as its maximum width is commonly

at the hinge-line. The plano-convex profile is like that of *Tapajotia* but different from the dorsi-biconvex profile of *Derbyoides*. The external radial ornament, with about 11 ribs in 5 mm. at 10 mm. antero-medianly of the dorsal umbo, is of much the same frequency as that of the American genera. However, the form of the ribbing does vary. *Brochocarina* is parvicostellate with narrow, rather angular ribs which only attain their full dimensions after about 5 mm. (First order costellae attain full size after 3 or 4 mm. while second and third order costellae only attain full size after about 10 mm., if at all.) This led to the development of relatively wide inter-spaces, especially posteriorly, and this contrasts with the more regular, rounded radial ornament of the other two genera.

Thus, *Brochocarina* may be distinguished principally by its ventral interior and narrowly divergent socket plates. *Derbyoides* differs in its convex and heavily thickened brachial valve and in having a medianly developed dorsal septum. The Fermanagh shells are older than the other genera of the subfamily, except for *Hipparionyx*, and yet show a stage of development of the ventral interior apparently intermediate to that of *Tapajotia* and *Orthotetes*. Of the presently described genera *Brochocarina* could have been ancestral to *Derbyoides* and *Tapajotia* by the reduction of the dental ridges in these later genera, and to *Orthotetes* by the increased deposition of secondary shell in this region.

Brochocarina wexfordensis (Smyth)

(Pl. 4, figs. 24-26, Pl. 5, figs. 1-23. Text-figs. 18-26)

1855 ?*Leptaena* (*Stromphomena*) *crenistria* (Phillips); M'Coy: 450.

1861 *Streptorhynchus crenistria* (Phillips) Davidson (pars): 124, pl. 26, fig. 5, (?2 and 6) non figs. 1, 3 and 4.

1930 *Schuchertiella wexfordensis* Smyth: 555, pl. 20, figs. 5-9.

1931 *Derbyia ambigua* Muir-Wood (pars): 144, fig. 3, non pl. 10, figs. 4, 5.

DIAGNOSIS (emended). Outline subsemicircular, with length about two-thirds maximum width; radial ornament unequi-parvicostellate with about 6 ribs in 2.5 mm. width, 5 mm. antero-medianly from dorsal umbo, interrupted by occasional growth lamellae, growth-lines numerous; pseudodeltidium arched with apical angle about 65°, flanked by wide perideltidium with apical angle about 130°, teeth prominent, adult dental ridges deep, almost reaching floor of valve; socket plates low, about one-quarter hinge width, recurving posteriorly to floor of valve.

MEASUREMENTS (in mm.):

		length	width
HOLOTYPE.	Complete brachial valve (T.C.D.196/1086)	36.3	c. 49.6
PARATYPE.	Incomplete pedicle valve (T.C.D.199/1086)	—	63.5
	Incomplete pedicle valve (BB.52732)	—	67.9
	Incomplete pedicle valve (BB.52734)	c. 11.0	—
	Incomplete brachial valve (BB.52735)	—	c. 9.5
	Complete brachial valve (BB.52736)	32.3	c. 53.0
	Complete crushed shell (BB.52738)	c. 64.0	c. 90.0

LOCALITIES AND HORIZONS: Holotype and paratype: Smyth Collection Nos. 196/1086, 199/1086 at Trinity College, Dublin, collected from Lower Carboniferous rocks on the west side of Hook Head, Co. Wexford. ?C₁.

BB.52732-52736: Subreefal limestones and shales of Bunnahone and Carrick Loughs, 2 miles N.W. of Derrygonnelly, Co. Fermanagh. D₁. BB.52738: Bundoran shales, Bundoran, Co. Donegal. S₂.

DISCUSSION. In all known respects the present Fermanagh material agrees with the type specimens of *Schuchertella wexfordensis* Smyth, 1930, from upper Tournaisian and lower Viséan beds of Hook Head, Co. Wexford. Although a statistical comparison of the growth axes "a" for the Hook Head and Fermanagh specimens indicates that there is a slight significant difference ($0.02 < p < 0.05$), the ventral interiors are identical (cf. Pl. 4, fig. 24 with Pl. 5, fig. 13) and no differences can be distinguished between the external ornamentation. The two are, therefore, considered to be conspecific.

In 1931 Muir-Wood (in Garwood) described a new species of davidsoniacean, *Derbyia ambigua*, from C₂ beds in Roxburghshire. Five of the original specimens are in the British Museum (Nat. Hist.), but they are not all conspecific and two (B.56425, B.56410) are thought to be conspecific with Smyth's species while a third fragment (B.56415) is probably conspecific. The holotype of *D. ambigua* (B.56411) and the pedicle valve interior (B.56416) figured (1931, pl. 10, fig. 5) are distinctive. Without brachial valve interiors it is difficult to be certain about the generic designation, but the high ventral median septum and small delthyrial cavity are more reminiscent of *Orthotetes* than *Derbyia*.

The description of *Leptaena (Strophomena) crenistria* (Phillips), given by M'Coy in 1855 (: 450) is in agreement with the present species in all recorded features. However, it is not conspecific with *Spirifera crenistria* Phillips (1836 : 216) which has a convex brachial valve (pl. 9, fig. 6) and is assigned correctly by Thomas to *Schellwie-nella* (1910 : 126). The illustration of *Streptorhynchus crenistria* (Phillips) by Davidson (1861, pl. 26, fig. 5) has been variously ascribed; to *Schuchertella* by Thomas (1910) and Smyth (1930 : 555), and to *Tapajotia* by Dresser (1954 : 37). Dresser considered Davidson's specimens to be "specifically distinct from *T. tapajotensis* because they possess a much deeper impression of the muscle scars in both valves". This observation could be used to separate the present species from that illustrated by Davidson. It should be remembered, however, that his specimen illustrated in fig. 5 is from Hook Head, the type locality, and that several of Davidson's illustrations are somewhat stylized. It may be that Davidson's figs. 2 and 6 (cf. pl. 26) are also conspecific.

The species differs from *Schuchertella pseudoseptata* Campbell (1957 : 46), described by him as closely resembling *S. wexfordensis*, by not having socket plates which are parallel to the hinge-line. Campbell's species apparently never reached the dimensions of *S. wexfordensis*, and from the description is only comparable in its ventral muscle field and septation.

Growth of the shell was almost equally radial to give a high coefficient of correlation between length and width ($r = 0.998$). The greatest width is almost invariably at the hinge-line, so that the cardinal extremities remain at 90° or less. Costellation

is probably a reflection of setal growth at the mantle margin, and as such remains constant throughout several genera of the davidsoniaceans. As in other genera, the costae number sixteen to eighteen on each valve, one to four orders of costellae being regularly and symmetrically intercalated so that in a width of 2.5 mm. antero-medially of the dorsal umbo the costellae are arranged as in Table 8. Because of the flatness of these shells, and the frequency with which their anterior margins are broken, the best estimate of shell thickness is gained by measuring the height of the delthyrium (Table 11). From the complete specimens available it is clear that this posterior region represents the region of greatest shell depth.

Fine growth lines form minute ridges across the crests of the costellae which became increasingly prominent anteriorly, until in adult shells, the ridges are prolonged into small spinose lamellae Pl. 5, fig. 12. Concentric lamellae, formed by interruptions in growth, are variably developed, although they tend to be concentrated towards the adult shell margins, presumably because of reduced shell growth.

An unusual characteristic of the species, is the way in which the brachial valve commonly becomes flat, or slightly concave, over a distance of about 10 mm. immediately anterior to the initial convexity of the umbonal region. The perideltidium, which is best seen on calcareous shells (Pl. 5, fig. 19), extends laterally for about one-half the width of the ventral interarea and is finely striated vertically, as well as bearing the sporadic growth lines that traverse the whole interarea and pseudodeltidium. It is possible that a similar area occurs upon the dorsal interarea. Clearly the periostracal shell covering was differentiated in the perideltidial region and the fine vertical striations are suggestive of a tight bonding to the shell surface, as might be expected under a periostracal pad (Williams 1956 : 257).

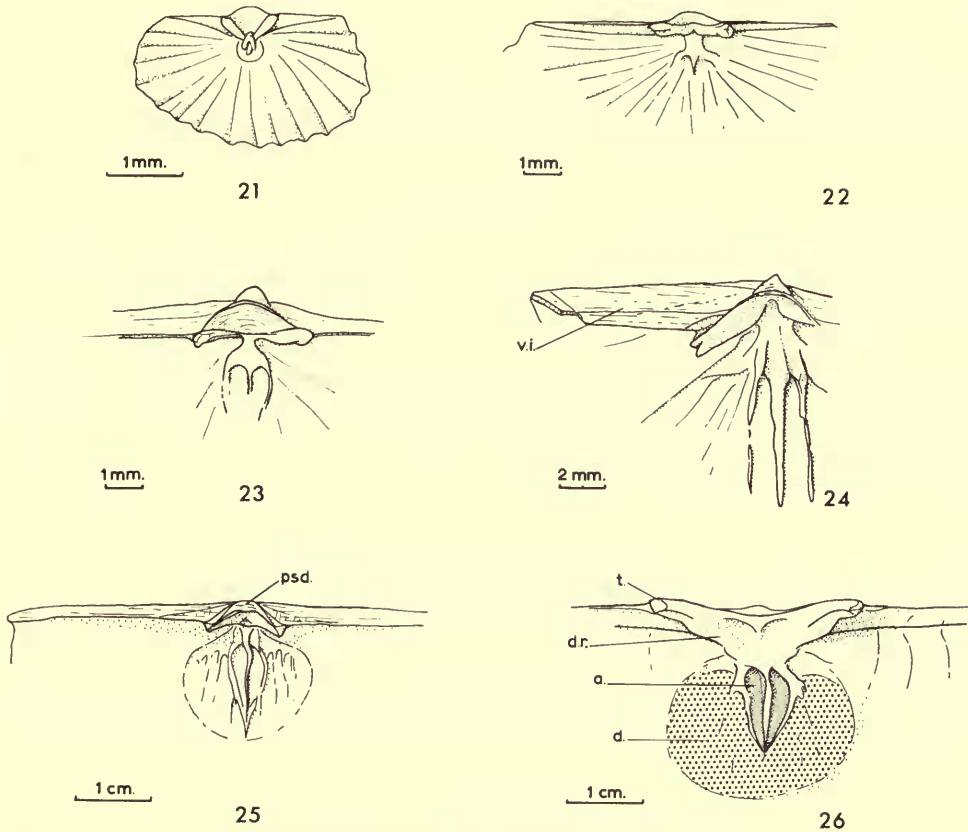
The chilidium is best seen in adult shells, (Pl. 5, figs. 6, 18) but its development can be followed from shells only about 3 mm. wide. In adult shells, with a dorsal interarea 1.5 mm. long, the chilidium curves around the base of the cardinal process lobes and is separated from them laterally by prominent grooves. A short chilidial ridge supports the structure between the cardinal process lobes and laterally it merges with the socket plates.

Internally, the margins of adult shells are commonly secondarily thickened to a greater extent than the remaining surfaces, but never to the extent of those of *Derbyoides nebrascensis*. This thickening, together with the closely spaced external lamellae at the shell margin, indicates periodic mantle retraction. This process increased both the thickness of shell substance and the total depth of the shell without appreciable increase to shell length or width.

The development of the dental and median ridges is informative in indicating the affinity of these shells with stratigraphically younger forms, and helps to confirm the interpretation by Williams (1965 : H404) of the delthyrial chamber of *Orthotetes* Fischer de Waldheim. The low trifid median ridge, which separates the ventral adductor scars from the diductor scars, arose umbonally and fused with the posterior ends of the dental ridges as a result of secondary shell deposition (Text-figs. 21-26). Shell deposition in adult stages increased the depth of the dental ridges until they approached the floor of the valve posteriorly (Text-fig. 26). Continued shell deposition umbonally could have buried the posterior ends of these ridges, together

with the median ridge, so that in cross-section the ventral beak might appear to possess a thick "pseudospondylium".

A study of dorsal interiors varying from 1.5 mm. to 55 mm. wide shows certain changes in the cardinalia. The angle of the socket plates to the hinge-line varies, tending to decrease slightly with age. In an assemblage of variously sized shells the



FIGS. 21-26. Illustrations of the ontogeny of the pedicle valve interior of *Brochocarina wexfordensis* (Smyth), postero-ventral aspect, showing the fusion of the dental ridges with the median septum. *a*, adductor scar; *d*, diductor scar; *d.r.*, dental ridge; *psd.*, pseudodeltidium; *t*, tooth; *vi.*, ventral interarea.

angle is commonly between 20° and 25° . The smallest shells show scarcely any inter-area, the cardinal process is but slightly differential into two lobes, the socket plates are straight, (Pl. 5, figs. 20, 21) and there are only the slightest lateral swellings indicating the origins of the chilidium. By a width of 4.5 mm. all the essential elements of the cardinalia are distinguishable, save for the median ridge and ventral node between the cardinal process lobes and the slight thickening between the socket plates, bounding the postero-median edges of the subcircular adductor field (Pl. 5, fig. 22).

TABLE 8

No. of ribs	4	5	6	7	8
A	0	4	6	3	3
B	2	5	3	1	0

TABLE 8. The number of ribs counted in 2.5 mm. (A) and 10 mm. (B) antero-medially of the dorsal umbo of *Brochocarina wexfordensis* (Smyth).

TABLE 9

\bar{l} mm. (var.) = 6.33 (77.093)	\bar{w} mm. (var.) = 10.03 (213.866)
\bar{w} mm. (var.) = 10.03 (213.866)	\bar{s} mm. (var.) = 2.63 (8.032)
$r = 0.998$	$r = 0.997$
a (var.) = 1.666 (0.00111)	a (var.) = 0.194 (0.000023)

TABLE 9. Statistics of length (l), maximum width (w) and maximum width of the socket plates (s) of 12 dorsal valves of *Brochocarina wexfordensis* (Smyth) from Co. Fermanagh.

TABLE 10

\bar{l} mm. (var.) = 26.60 (70.203)
\bar{w} mm. (var.) = 38.61 (137.950)
$r = 0.983$
a (var.) = 1.402 (0.01114)

TABLE 10. Statistics of length (l) and maximum width (w) of 8 pairs of measurements from type dorsal valves of *Brochocarina wexfordensis* (Smyth) from Hook Head, Co. Wexford.

TABLE 11

\bar{l} mm. (var.) = 9.56 (122.115)	\bar{l} mm. (var.) = 9.56 (122.115)
\bar{w} mm. (var.) = 12.96 (226.31)	\bar{h} mm. (var.) = 1.29 (1.652)
$r = 0.994$	$r = 0.956$
a (var.) = 1.361 (0.00079)	a (var.) = 0.116 (0.00042)
\bar{h} mm. (var.) = 1.29 (1.652)	
\bar{d} mm. (var.) = 1.83 (3.873)	
$r = 0.984$	
a (var.) = 1.531 (0.00268)	

TABLE 11. Statistics of length (l), maximum width (w), height of delthyrium (h) and width of delthyrium (d) at the anterior margin of the interarea of 16 pedicle valves of *Brochocarina wexfordensis* (Smyth) from Co. Fermanagh.

?Orthotetimid gen. and sp. indet.

(Pl. 7, figs. 1-7)

Three distinctive cardinalia have been recovered from the etched limestones of the Sillees River, Bunnahone, but no pedicle valves are known. Fortunately the three vary in size, viz. total widths of socket plates = 4.7 mm., 14.1 mm. and 17.6 mm., allowing ontogenetic changes to be observed. These cardinalia are quite unlike other davidsoniacean species from the faunas and are unusual in their slight strophomenacean characteristics, i.e. external ornament and strong dorsal median septum. A cardinalia figured by Davidson (1861, pl. 27, figs. 6, 7) from Settle, Yorkshire is probably conspecific, but was included as *Streptorhynchus crenistria*; otherwise comparable material does not appear to have been described.

The brachial valve was apparently gently convex with a wide straight hinge-line, well developed anacline interarea and arching chilidium from below which the cardinal process projected strongly. The external ribbing occurs with a frequency of about 10 ribs in 5 mm. width, 5 mm. from the umbo, and is apparently parvicostellate. Between the ribs is a less distinct concentric ornamentation of minute ridges (Pl. 7, fig. 1), similar to that of strophomenaceans.

Internally the cardinal process is typically davidsoniacean with two well developed incised lobes between which is a chilidial ridge terminating ventrally in a node. The socket plates are strongly recurved and nearly parallel to the interarea; medianly they merge to the cardinal process and prominent median septum, which is present even in the smallest specimen.

The lack of pedicle valves make it impossible to be quite sure of familial placing but the form of the socket plates indicates either the Schuchertellinae or Orthotetinae as the most likely subfamilies. Of these the latter group seems more appropriate as some members of the Orthotetinae have a poorly developed dorsal median septum. Until more material is available, in particular matching pedicle valves, a full generic or specific designation will not be attempted.

Family **SCHUCHERTELLIDAE** Williams 1953

Subfamily **SCHUCHERTELLINAE** Williams 1953

Genus **SERRATOCRISTA** nov.

DIAGNOSIS. Shell small, commonly ventribiconvex, pedicle valve strongly curved to conical in young shells; hinge-line straight, commonly approximating to maximum width; ventral interarea elongate, apsacline to catacline, pseudodeltidium arched and entire, perideltidium obscure; dorsal interarea and chilidium much reduced; radial ornament multicostellate, spinose with costellae regularly intercalated; teeth supported by low dental ridges; muscle scars indistinct, rarely with slightly raised lanceolate adductor scars; cardinal process low, bilobed and supported by widely divergent socket-plates at about 25° to hinge-line; adductor field obscure, shell substance probably pseudopunctate.

TYPE SPECIES. *Serratocrista fistulosa* sp.n.

DISCUSSION. *Serratocrista* is included in the subfamily Schuchertellinae on account of its typically schuchertellid dorsal interior, including socket plates which diverge from the hinge-line acutely and which recurve slightly at their antero-lateral extremities. This is in contrast to the socket plates typical of the Streptorhynchinae, which diverge from the hinge-line less acutely, at 50° to 60°, and continue antero-laterally fused to the brachial valve floor with no recurvature towards the posterior margin. *Serratocrista* differs from *Schuchertella* Girty, in being pseudo-punctate and having no dorsal median ridge, features which recall *Orthopleura* Imbrie, although it differs from this genus in being multicostellate and "spinose". Unlike *Schuchertellopsis* Maillieux, representatives of the new genus were not completely cemented by their pedicle valves to a foreign body during their life.

Serratocrista fistulosa sp.n.

(Pl. 6, figs. 1-12)

DIAGNOSIS. Biconvex Schuchertellinae bearing spinose, strong ribs; chilidium obsolescent, weak dental ridges and poorly impressed muscle scars.

DESCRIPTION. Outline transversely semi-oval, approximately two-thirds as long as wide; biconvex, one-third as thick as long, slight dorsal median sulcus; strongly multi-costellate bearing about four crestal "spines" medianly between 9 and 10 mm. from dorsal umbo. About eight ribs occur per 2.5 mm. width antero-medianly at 5 mm. from dorsal umbo, pedicle valve costae commonly slightly stronger than costellae; ventral adductor scars posteriorly placed, lanceolate, enclosed by slight ridges; cardinal process low, lobes well separated by sulcus, socket plates diverge from hinge-line at about 25°, prominent anteriorly, reaching almost one-third width of hinge-line; sockets arched postero-medianly by antero-lateral growth of vestigial chilidial plates; median septum absent, adductor scars obscure.

MEASUREMENTS (in mm.):

		length	width
HOLOTYPE.	Complete shell (BB.52739)	14.4	18.0
PARATYPES.	Complete brachial valve (BB.52740)	9.6	14.6
	Complete pedicle valve (BB.52741)	14.1	20.0
	Complete pedicle valve (BB.52744)	3.6	5.1

TYPE LOCALITY. Sillees River, about 300 yds. east of Bunnahone Lough (low D zone).

DISCUSSION. The costellate ornamentation is distinctive with its short pointed "spines" commonly arising alternately from the crests of the ribs (Pl. 6, fig. 3). These "spines" become slightly more widely spaced anteriorly, but medianly between 9 and 10 mm. from the umbo there are about four. Costellae were added by branching and intercalation, although the latter is rare on pedicle valves and the branching is predominantly median in origin. The costellae approximate to the size of the costae within about 5 mm. of their origin. At 5 mm. from the umbo 3, 3

and 9 valves have 6, 7 and 8 ribs per 2.5 mm. width antero-medianly. The ribbing is prominent with rounded crests and straight or slightly concave sides, up which fine growth-lines can be traced (Pl. 6, fig. 3), and both wave-length and amplitude of the ribs are commonly about equal. The radial ornamentation is comparable to that of the mid Devonian European species *Xystostrophia umbraculum* (Schlotheim); both species developed spinose outgrowths from their ribs, but in other respects, such as cardinalia, the two are quite distinctive.

The shell interiors are unusually featureless, despite secondary thickening; the dental ridges show no accentuation with increased age, nor is there any sign of a median ridge in either valve.

Although described as pseudopunctate, the shell structure is a little uncertain. The internal surfaces, of pedicle valves in particular, are covered by small pits which are confined neither to ribs nor interspaces. Unfortunately, unsilicified material is not available so microscopic examination of unaltered shell is impossible. One incompletely silicified specimen is broken across the ventral interarea and part of the valve. The inner and outer surfaces are completely silicified but internally there is only a silica lattice comprising lamellae held by more or less perpendicular fine rods (Pl. 6, fig. 11). This structure may be interpreted as being selective silicification along planes in the original shell structure which represented a form of punctation and the shell lamellae. Thomas (1958) describes Permian *Streptorhynchus* from Western Australia as having a shell structure that differs from his other Davidsoniaceae. The conical flexures of the shell lamellae are directed outwards, rather than inwards as in normal pseudopunctate shells, and Thomas suspects that these flexures surrounded a fine canal (Thomas 1958, pl. 19). In the Australian material this "punctation" was confined to the ribs, as is the internal punctation of many enteletaceans and terebratuloids.

If the shell structure of the Fermanagh material was comparable it would explain the minute pits on internal surfaces and could explain the selective silicification of the shell figured in Plate 6, fig. 11.

TABLE 12

\bar{l} mm. (var.) = 10.83 (17.530)	\bar{l} mm. (var.) = 10.83 (17.530)
\bar{w} mm. (var.) = 14.52 (31.078)	\bar{th} mm. (var.) = 3.02 (0.654)
$r = 0.970$	$r = 0.893$
a (var.) = 1.332 (0.0262)	a (var.) = 0.193 (0.0022)

TABLE 12. Statistics of length (l), maximum width (w) and thickness (th) of 6 pedicle valves of *Serratocrista fistulosa* sp. n.

TABLE 13

\bar{l} mm. (var.) = 5.75 (12.22)
\bar{w} mm. (var.) = 8.33 (23.551)
$r = 0.988$
a (var.) = 1.389 (0.0058)

TABLE 13. Statistics of length (l) and width (w) of 10 brachial valves of *Serratocrista fistulosa* sp. n.

Family **MEEKELLIDAE** Stehli 1954

Subfamily **MEEKELLINAE** Stehli 1954

[= Omboniinae Sokolskaja 1960]

Genus **SCHELLWIENELLA** Thomas 1910

TYPE SPECIES. *Spirifera crenistria* Phillips 1836, by original designation of Thomas (1910 : 92).

Schellwienella radialis (Phillips)

(Pl. 6, figs. 13-24. Text-figs. 27-35)

1836 *Spirifera radialis* Phillips: 220, pl. 11, fig. 5.

1861 *Streptorhynchus crenistria* var. *radialis* (Phillips) Davidson: 129, pl. 25, figs. 16, 17, 18.

1930 ?*Schellwienella* aff. *aspis* Smyth: 555, pl. 16, figs. 6a, 6b.

1934 ?*Schellwienella aspis* var. *radialiformis* Demanet: 85, pl. 7, figs. 6-12.

DIAGNOSIS (emended). Dorsibiconvex to slightly resupinate *Schellwienella* with strong parvicostellate ribbing, strong divergent dental plates, small complete chilidium, high cardinal process and deeply impressed dendritic dorsal adductor scars in adult.

DESCRIPTION. Profile inequibiconvex, adult brachial valve strongly convex posteriorly, thickness about one-half shell width; shell length about three-quarters width, adult anterior margin commonly slightly uniplicate; ribbing unevenly parvicostellate, commonly with seven ribs per 2.5 mm., 5 mm. antero-medially of dorsal umbo, costae consistently stronger than intercalated costellae; concentric lamellae, becoming crowded marginally; ventral interarea apsacline, pseudodeltidium arched, perideltidium indistinct; dorsal interarea short with chilidium of equal length; dental plates receding, diverging to floor of valve, posteriorly enclosing muscle field consisting of postero-medially placed adductor scars flanked by pair of rounded triangular diductor scars; cardinal process prominent, wide and bilobed; socket plates at about 50° from hinge-line and curved to valve floor to enclose sockets; in adults ridges extend from socket plates to enclose oval dendritic adductor scars separated by slight median ridge; shell substance sparsely pseudopunctate.

MEASUREMENTS (in mm.):

	length	width
HOLOTYPE. Brachial valve (E.2054)	c. 30.0	c. 42.0
Incomplete brachial valve (BB.52746)	c. 11.8	c. 15.4
Complete brachial valve (BB.52747)	30.6	42.0
Incomplete brachial valve (BB.52748)	c. 30.8	c. 40.0
Crushed, incomplete shell (BB.52750)	c. 50.0	c. 59.0

TYPE LOCALITY AND HORIZON:

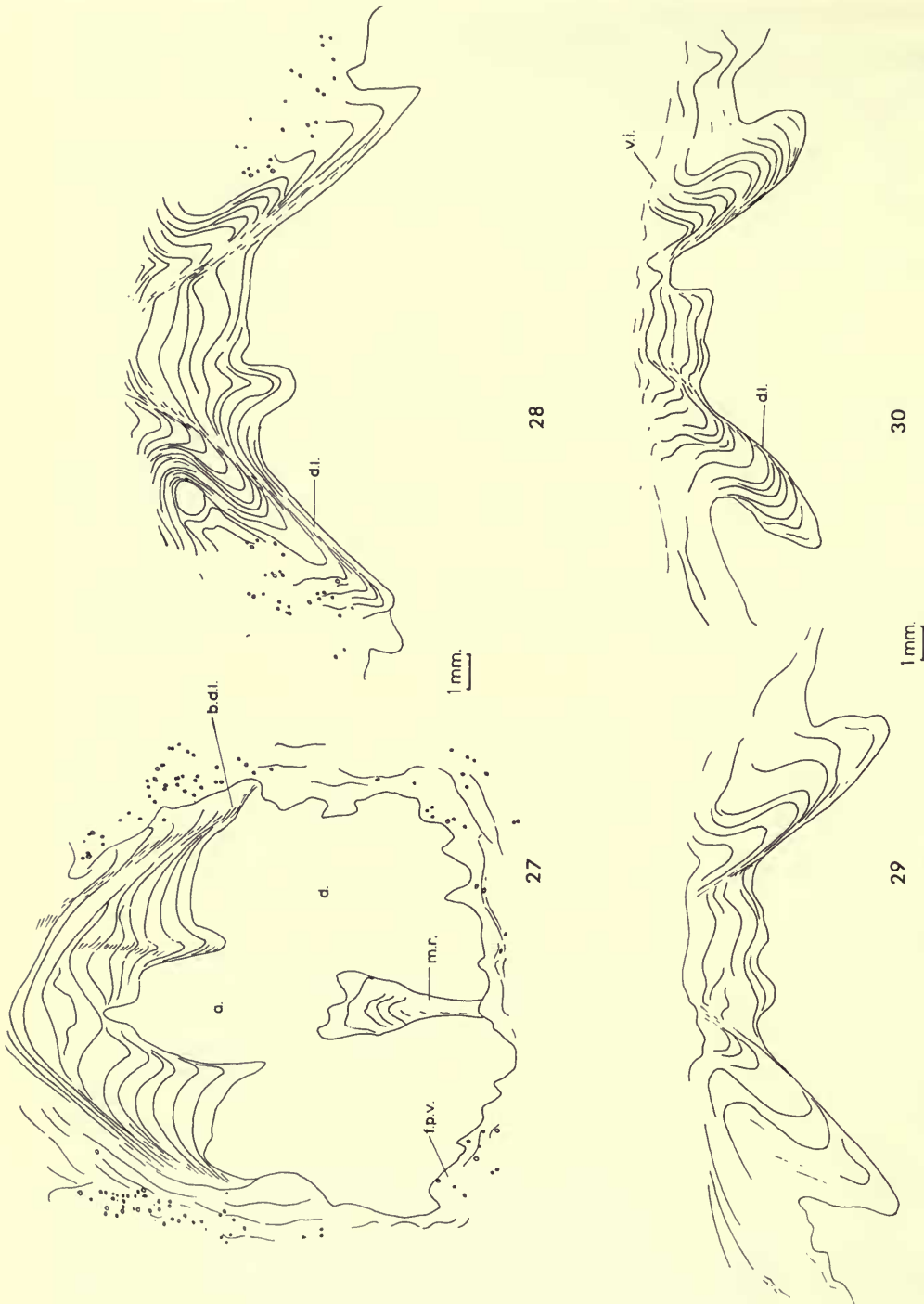
Holotype—in the University Museum, Oxford; No. E2054 collected by Phillips from the “Base of the upper Irish limestone” at Florence Court, about 12 miles S.E. of Derrygonnelly, Co. Fermanagh.

Other specimens from the argillaceous limestones and shales of Bunnahone and Carrick Loughs, 2 miles N.W. of Derrygonnelly, Co. Fermanagh, or from underlying shale $\frac{1}{2}$ mile upstream from Milltown Bridge, 1 mile N.W. of Church Hill, Co. Fermanagh. Low D. zone.

DISCUSSION. Although Thomas (1910 : 126) recorded the type material of *Spirifera radialis* Phillips as having been lost, the specimen figured by Phillips (1836, pl. 11, fig. 5) is actually preserved in the University Museum, Oxford, No. E.2054 and another specimen, No. E.2055, is possibly the second mentioned by Phillips on p. 220 as coming from Cumberland, but it is not as well preserved as the type specimen from Florence Court, Co. Fermanagh. Phillips described the Florence Court locality as being at the “Base of the Upper Irish limestone”, which is the lateral equivalent of the “reefal” limestones about 12 miles N.W., near Derrygonnelly, from below which the present material was collected. The lithology and fauna associated with the type specimen closely resembles the more shaly beds underlying the limestone horizon at Bunnahone from which the silicified fauna was collected. The type specimen itself shows only part of the dorsal exterior (Pl. 6, fig. 24), but in all known details it is closely comparable with the schellwienellas recovered from Bunnahone and for these reasons the horizons are considered comparable and the forms conspecific.

Thomas (1910 : 126) referred *Spirifera radialis*, “as ascribed by some British authors” to *Schuchertella*, a view followed by Demanet (1934 : 87) and Sarycheva & Sokolskaja (1952 : 43). One of Davidson’s figures, (1861, pl. 25, fig. 17) however, clearly shows schellwienellid dental plates in an illustration of *Streptorhynchus crenistria*, var. *radialis* from Gare, Lanarkshire, and it is probable that all three figures, viz. 16, 17 and 18, are of *Schellwienella radialis*. Short, but well developed dental plates are clearly visible in the Fermanagh specimens. (Text-figs. 27–30, Pl. 6, fig. 17)

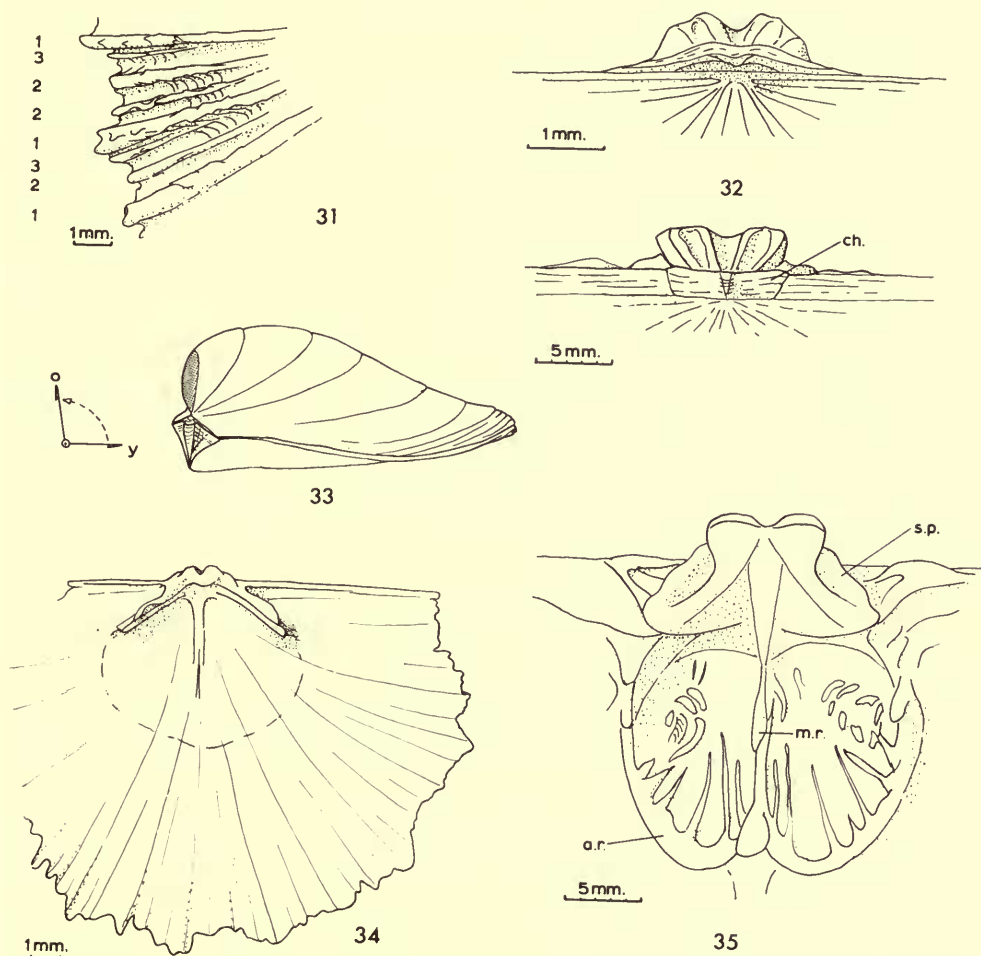
The differentiation between costae and intercalated costellae is clear in shells longer than 5 mm. The ribs are adorned by short dart-like projections, usually arranged alternately, one on either side of the rib crest, with a modal frequency of 3 per mm. between 4 and 5 mm. from the umbo. There is no clear correspondence between these serrations and the growth-lines, but the latter do project forward in crossing each rib, showing that growth was more rapid in this region (Pl. 6, fig. 19). In order to have maintained a more or less equally developed anterior margin, without greatly extended ribs, the mantle must have retracted more strongly at the rib crests than between them where shell deposition would have continued more evenly. This retraction of the mantle probably resulted in the formation of the spinose serration. The ornament contrasts with the undifferentiated ribbing arrangement of *Schellwienella aspis* Smyth, from Hook Head, Co. Wexford, in rocks of K, Z and C age. Smyth (1930 : 555), however, says that there is a tendency for



FIGS. 27-30. Illustrations of sections parallel to the commissural plane of the ventral umbonal region of *Schellienella radialis* (Phillips). Pseudopunctate inner shell material surrounds the central space within which the ventral muscle bases were accommodated. The dental plates can be seen to fuse with the floor of the pedicle valve. *a*, adductor muscle region; *b.d.l.*, base of dental plate; *f.p.v.*, floor of pedicle valve; *m.r.*, median ridge separating the paired muscle scars; *v.l.*, ventral interarea.

the costae of specimens from the strata of C age to be stronger and for "... every fourth one to be emphasized". Thus, it is possible that the ornamentation became more differentiated through strata of C and S age to that seen on *S. radialis* in Upper S and D strata.

The chilidium is well formed and in a brachial valve 11 mm. long was 2.7 mm. wide and 0.3 mm. long (Text-fig. 32) arching over the posterior face of the cardinal process in a postero-dorsal direction. A rudimentary chilidium can be distinguished



FIGS. 31-35. Illustrations of *Schellwienella radialis* (Phillips) showing the morphology of the external radial ornamentation, (Fig. 31); the chilidium of young and adult specimens (Fig. 32); a lateral view of an adult shell and the rotation of the juvenile portion of the shell (stippled) relative to the hinge line (Fig. 33); and the cardinalia, viewed dorsally, in young (Fig. 34) and adult (Fig. 35) specimens. 1, costae; 2, first order costellae; 3, second order costellae; *a.r.*, ridge surrounding the adductor scars; *ch.*, chilidium; *m.r.*, median ridge; *s.p.*, socket plate.

in valves only 2.5 mm. wide, as bulbous projections postero-laterally of the cardinal process lobes, similar to those seen in *Brochocarina wexfordensis*. During growth the distal edge of the chilidium became directed posteriorly and finally ventrally. This resulted not so much from a differential growth of the chilidium itself but by the progressive rotation of the dorsal hinge-line resulting from increasing valve convexity (Text-fig. 33), and the considerable thickness of secondary shell at the anterior margins of gerontic valves. This angle of rotation may exceed 90° and in a specimen 52 mm. long approaches 110° . The cardinalia is typically davidsoniacean in young shells (Text-fig. 34) but became considerably thickened in old age. In adult shells the anterior face of the cardinal process became thickened so as to extend beyond the youthful socket plates, leaving a distinct groove between the two. The socket plates extend antero-laterally from the hinge-line at about 45° to 55° enclosing the sockets medianly. Although the bases of the socket plates curve to the valve floor to bound the sockets antero-dorsally, they do not recurve towards the hinge-line as in Orthotetinae. In shells more than about 40 mm. wide shell deposition formed ridges which extended from the socket plates around the adductor field. Postero-laterally within each adductor scar is an oval area, about one-third as long as the complete scar, which has a differentiated ornamentation and may have been the scars of posterior adductor muscles (Pl. 6, fig. 22).

In comparing the socket plates of different davidsoniacean subfamilies it must be recognized that while those of the Meekellinae are described as prolonged, as are those of the Streptorhynchinae and Derbyiinae, they do curve to the valve floor in a manner similar to the Schuchertellinae. However, the socket plates of the Schuchertellinae diverge from the hinge-line at a narrower angle than do those of the Meekellinae, while in the Orthotetinae they recurve towards the hinge-line with little anterior fusion to the valve floor.

Superfamily CHONETACEA Bronn 1862

The chonetacids are not considered to be a separate suborder, but to be sufficiently closely related to the Productacea to belong to the suborder Productidina. Muir-Wood (1962) discussed the classification of the chonetacids and followed her earlier works of 1955, and with Cooper 1960, by separating them from the Productacea in the belief that productaceans never had a functional pedicle. This has been shown to be incorrect (Brunton 1965) and at least some genera of both groups had functional pedicles during their earliest stages of ontogeny. A pedicle sheath was previously unrecorded from chonetacids above the Devonian but is now described in Fermanagh rugosochonetids and globosochonetids of Visean age.

It seems probable that Sarycheva & Sokolskaja (1959) are correct in uniting the Chonetacea and Productacea and their reversion to the previously held view that the Productacea were derived from the Chonetacea warrants careful consideration. The two groups are united by a comparable gross morphology, pseudopunctuation and spine development and also by a similar phylogenetic trend to gigantism in the Lower Carboniferous. This may indicate a response to certain conditions by groups of organisms having arisen from the same ancestral gene pool. Probably during the

Devonian period the Productacea and Strophosiaacea differentiated from a chonetacean-like stock and rapidly diversified.

The plectambonitaceans possibly provided the ancestral stock from which the chonetacids arose, possibly late in the Ordovician. Some of the earliest strophochonetids, from Anticosti Island, Canada, are from beds commonly correlated with the Upper Llandovery or Lower Wenlock. *Eochonetes advena* Reed, described from the Upper Ordovician, Drummuck Group of Girvan, is plectambonitid in character but had hollow canals, passing from the interior towards the exterior of the posterior margin, which closely resemble the canals leading to the spines of Chonetacea. It is not known whether the canals of *Eochonetes* extended to the outer surface, and spines are unknown. But it is no great evolutionary step for the epithelial processes, or evaginations, already present in *Eochonetes* to have remained generative at their tips and to have grown posteriorly, accompanied by the deposition of shell so as to have formed spines.

Rib apertures have been observed and figured from the time of Davidson's monograph (1861) to Muir-Wood's recent chonetoid monograph (1962) in which she follows Dunbar & Condra (1932) in assuming that they are the bases of minute hollow spines. Muir-Wood (1962, pl. 6, fig. 6) illustrates the impression of the pedicle valve of a rugosochonetid which is said to show "spinules". However, inspection of the specimen (BB.20424) shows that fragments of shell adhere to the mould from which taleolae or endospines protrude. Besides these there are fine obliquely disposed ridges of sediment aligned along the rib impressions. These are the sedimentary infillings of the rib apertures ("spinule bases"), but neither they nor the taleolae are "spinules" protruding from the outer shell surface. A similar phenomenon has been recorded by Demanet (1934 : 52) on moulds of *Schizophoria*, where infillings of the punctae by iron oxides have left a minutely spinose surface. On no specimens, either from Fermanagh or those studied by Davidson (1884, pl. 20, fig. 21), have actual "spinules" been observed and it seems more likely that a rib aperture was never the base of a true spine. The formation of the apertures probably took place by the sporadic inward sag of the mantle edge from the shell surface, and the resulting oblique hollows became sealed at their inner ends by the deposition of secondary shell. Anterior to each aperture, as growth continued, the rib regained its shape by the reversion of the mantle edge to its normal folded condition.

The morphology of the chonetacid hinge spines has attracted attention and it is generally agreed that their formation was as described by Williams (1956 : 252). However, Muir-Wood (1962 : 5) considers that chonetid spines differ from productacid spines in that the latter were open at their distal end. Evidence in support of this inference is lacking and it seems more reasonable, since the spines of both groups were capable of growth, that the distal ends were sealed by the generative tip of epithelium, covered by periostracum. The angle of emergence of the spines from the hinge-line varied during the growth of the shell and they commonly curved so that the distal part of the spine was at a different angle from that at which it arose from the posterior margin. The early formed, more medianly placed spines, tend to have a higher angle to the hinge-line than have those towards the lateral

extremities. A feature of spine orientation, noted on the Fermanagh shells, is that the spines commonly extended posteriorly at the time of their origin. As a result of valve curvature, and consequent rotation of the shell relative to the substratum, the spines did not all grow parallel to the adult commissural plane. Thus, on adult shells the median spines may be dorsally directed while those towards the lateral extremities are progressively more posteriorly directed. This pattern of spine growth probably assisted in the stabilization of the shells on the substratum throughout life and after the pedicle had ceased to be functional.

Superfamily **CHONETACEA** Bronn 1862 *nom transl.* Shrock & Twenhofel 1953

Family **CHONETIDAE** Bronn 1862

Subfamily **ANOPLIINAE** Muir-Wood 1962

Genus **GLOBOSOCHONETES** nov.

DIAGNOSIS. Small, strongly concavo-convex Anopliinae with strong ribbing and pair of ventrally serrated, anteriorly divergent septa in brachial valve.

DESCRIPTION. Shell small, outline semi-elliptical with rounded prominent umbo, hinge-line widest part of shell; profile highly concavo-convex, medianly arched, adult shells with four pairs of spines at high angle to hinge; young furnished with pedicle sheath; multicostellate, commonly comprising sixteen costae branching dichotomously or with rarely intercalated costellae, ribs rounded and more prominent on pedicle valve; ventral interarea orthocline, narrow with open delthyrium and indistinct arched apical pseudodeltidium, dorsal interarea rarely developed; teeth short and poorly differentiated from ventral interarea; median septum high, posteriorly confined but commonly extended anteriorly as low ridge for about one-third valve length; radially arranged tubercles correspond to external intercostal spaces; cardinal process undifferentiated internally, externally with V-shaped myophore laterally supported by elongate, low socket ridges, almost parallel to hinge-line; short lateral septa variable developed; pair of high septa cross dorsal visceral disc almost to anterior margin, at about 12° from mid-line; adductor scars indistinct, divided by lateral septa; radially tuberculate as dorsal valve; shell pseudopunctate.

TYPE SPECIES. *Globosochonetes parseptus* sp. n.

DISCUSSION. The small size of these shells, together with their great convexity and pair of prominent plate-like accessory septa across the dorsal interior, are features common to genera included by Muir-Wood (1962) in her subfamily Anopliinae. Although these genera are all described as having smooth shells, save for growth lines, she does appear to allow for costellation in her subfamilial diagnosis by saying "shell normally smooth", (1962 : 32). Thus the new genus, *Globosochonetes*, is here included within the Anopliinae and differs from *Anoplia*, *Anopliopsis*, *Chonetina*, *Notanoplia* and *Tornquistia* in being strongly ribbed. The ribbing and arrangement of internal tubercles is intimate, so that while the latter are more or less scattered within smooth genera, they are radially arranged in *Globosochonetes*. The genus differs from *Plicochonetes*, of the Rugosochonetinae, with which it may have been

confused in the past, by its poorly differentiated cardinal process, strong dorsal septa, finer ribbing and smaller size.

Globosochonetes parseptus gen. et sp. n.

(Pl. 7, figs. 8-27, Text-figs. 36-41)

DIAGNOSIS. As for genus.

DESCRIPTION. Small, deeply convex shells, one-third as deep as wide, four-fifths as long as wide, with narrow body cavity; ventral umbo of young shells flattened or grooved, provided with supra-apical pedicle sheath; costation rounded, even and prominent except on umbones, costellae commonly dichotomously branched within first 2 mm. of ventral beak; five ribs occur in 1 mm. width, 2 mm. antero-medially from ventral umbo; adult hinge-spines slightly recurved towards mid-line, increasing in size laterally, ventral median septum prominent and thickened in beak adjacent to cardinal process; adductor scars oval, posteriorly placed, flanked by anteriorly spreading diductor scars; poorly differentiated cardinal process with small alveolus bordered by median ends of socket ridges that extend about one-half valve width and enclose shallow sockets; lateral septa indistinct, at about 45° to hinge-line and separate poorly defined posterior adductor scars from anterior adductor scars; pair of high accessory septa diverge from mid-line at 10° to 15°, serrated distal edges commonly exaggerated in geronitic shells; small, posteriorly placed, lobate median septum developed late in life.

MEASUREMENTS (in mm.):

	length	width
HOLOTYPE. Complete shell (BB.52751)	3.1	4.1
PARATYPES. Complete pedicle valve (BB.52752)	3.5	4.8
Incomplete brachial valve (BB.52753)	2.7	—
Complete brachial valve (BB.52755)	1.3	1.6
Incomplete pedicle valve with pedicle sheath. (BB.52756)	—	3.5
Incomplete pedicle valve with pedicle sheath. (BB.52757)	—	1.7
Incomplete brachial valve (BB.52754)	—	3.9
Complete shell (BB.55498)	3.7	4.4
Brachial valve (BB.55499)	c. 1.9	c. 2.6
Incomplete shell (BB.55783)	3.1	3.6

TYPE LOCALITY. Sillees River, about 300 yds. east of Bunnahone Lough (low D zone).

DISCUSSION. Two small specimens in the Davidson Collection of the British Museum (Nat. Hist.) (B.14174) from Settle, Yorkshire, which are possibly the originals for figure 18, plate 47 of Davidson (1861), are externally indistinguishable from the Fermanagh shells. Both have the same shape and rib counts. Although

the interiors of the Davidson specimens are not known, they are thought to be conspecific with *G. parseptus*.

The Fermanagh species is apparently similar to *Chonetes minuta* Goldfussi *sensu* de Koninck (1847 : 219, pl. 20) from the Devonian Eifel region. However, *C. minuta* is longer (length is given as 12 mm. by de Koninck) and the ribbing apparently more coarse, i.e. 22 ribs in all. *G. parseptus* is comparable in size and shape to *Leptaena* (*Chonetes*) *subminima* M'Coy. However, inspection of the type specimens from the Sedgwick Museum, Cambridge (E.6773-6780) shows that M'Coy's species has a finer costellation, viz. about 14 ribs per one mm., 1 mm. antero-medially from the ventral umbo (cf. Table 14). The poorly preserved dorsal interior shows no sign of the strong septa present in the Fermanagh species and the two are not conspecific. Neither is M'Coy's material conspecific with the specimen "from the Namurian of the river Hodder, Yorkshire" (B.53889) which Muir-Wood (1962 : 62) tentatively identified as "*Chonetes* [*Plicochonetes*] *subminimus* (McCoy)". The Hodder specimen has a rib count similar to that of *G. parseptus* and the two could be congeneric.

Tornquistia polita (M'Coy) resembles the new species in size, shape and dorsal interior but differs in being devoid of all ribbing.

Muir-Wood (1962 : 6) speaks of the young of some Devonian and Silurian chonetids having been attached by a pedicle which emerged through the ventral umbo and formed a "small pedicle pipe". The present Visean chonetids are probably the first of this age to be recorded showing the structure, here called the pedicle sheath. It was almost certainly not functional in valves 3 mm. long because the ventral beak of such valves is filled by secondary shell at the posterior end of the median septum. With a maximum diameter of only about 0.03 mm., it is unlikely that the pedicle was functional for long after the spat had settled, or that its growth continued beyond the neanic stage: certainly no internal opening has yet been distinguished in valves longer than 1.2 mm. The pedicle sheath is essentially the same structure as is seen in several genera of the productacea, and it does seem that a functional pedicle was more common in the early stages of brachiopod development than is often supposed. Unlike Muir-Wood (1962 : 6) the writer considers the pedicle sheath to be a feature of both strophomenoids and productoids, and one which indicates the close relationship of the two groups.

During growth, the rate of shell deposition appears to have been greatest on the flanks, so that the pedicle valve became highly arched medianly and in these regions occurred the greatest proliferation of the costae. In some shells this pattern of growth led to a slight flattening of the antero-median venter. Costae are absent from the first 0.5 mm. of the shell and less prominent upon the brachial valve. 2, 6, 12, 1 and 1 specimens have respectively 14, 15, 16, 17 and 18 costae. Branching most commonly occurred within the first 1.5 mm. from the pedicle beak and was usually of a dichotomous nature, especially on the pedicle valve. However, about three-fifths of the costellae of both valves were added by external, (i.e. lateral) branching or by intercalation, and any one specimen may show all these types of rib addition.

Of the four pairs of hinge-spines, the last formed are the largest, and although they arose from the hinge-line at an angle of about 120°, they soon curved inwards to

become parallel or even convergent to the mid-line. As would be expected, the spines arose at regular intervals, the third and fourth at valve lengths of about 2 and 3 mm. respectively. The means (with variances) of the distances between the spines are given in Table 15.

The first pair of spines were of very small diameter, like the pedicle sheath, and were soon internally sealed. The second pair remain open in valves about 1.2 mm. long, but beyond this size soon became closed by the antero-lateral growth of the interarea and teeth. The third and fourth pairs of spines commonly retain their internal connections, opening anterior of the interarea (Pl. 7, fig. 14). The teeth are commonly indistinctly differentiated from the interarea by a slight ridge, although in some specimens they are more distinct and diverge from the hinge-line at an angle of up to 10°.

The ventral median septum is distinguishable in valves 1.2 mm. long, and arose from the beak (Text-fig. 37). At this growth stage the adductor scars from a sub-rounded, rather flat area within the ventral umbo. Beyond this stage convexity was such as to reorientate the muscle field from being dorsally to anteriorly directed and within these adult shells the adductor field is divided by the septum, which, while remaining confined to the umbonal region, is extended anteriorly as a low ridge for nearly one-third the length of the valve (measured parallel to the commissural plane).

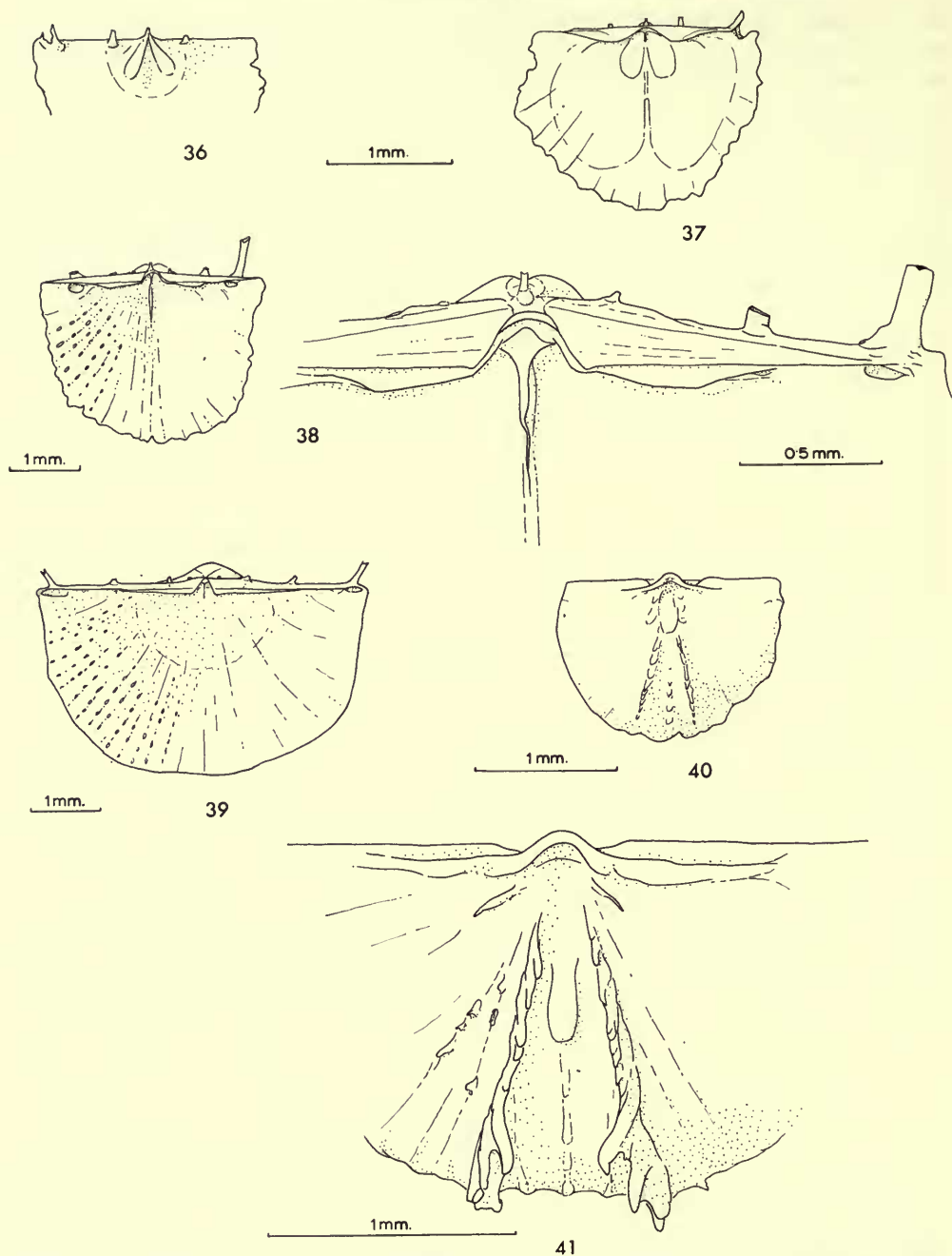
The protogular node is well seen on brachial valves, having been protected from abrasion by the shell convexity. It is commonly 0.3 mm. in length and about one-half the width, and is represented internally by the alveolus, lying between the cardinal process base, the socket ridges and the posterior ends of the strong accessory septa, which are 0.15 mm. apart (Text-fig. 40). The septa are highest at about mid-valve length and always have serrated distal margins, the serrations being anteriorly directed and lobate in gerontic shells (Text-fig. 41). These septa were probably supporting structures to the brachial apparatus and within these small shells may have assisted in the separation of the water currents in the brachial cavity.

A short median septum can be distinguished in dorsal valves of about 2 mm. in length. It continued to grow by secondary shell accretion over the median row of tubercles so that in valves about 3 mm. long it extended nearly 1 mm. anteriorly of the hinge-line. The alveolus always remained free of secondary structures (Pl. 7, figs. 21, 26).

TABLE 14

Ribs	4	5	6	7
A	0	23	41	10
B	8	21	6	0

TABLE 14. The number of ribs counted in a width of 1 mm. at 1 mm. (A) and 2 mm. (B) antero-medially of the ventral umbo of *Globosochonetes parseptus* gen. et sp. n.



FIGS. 36-39. Illustrations of the ontogeny of the pedicle valve of *Globosochonetes parseptus* gen. et sp. n., Fig 36 is the external view of the same specimen as Fig. 37 within which muscle scars, probably adductors, are clearly developed.

FIGS. 40-41. Brachial valve interiors of young and adult specimens of *G. parseptus*. The depression anterior to the cardinal process of the young valve is represented externally by the protugal node.

TABLE 15

	Between umbo and 1st	Between 1st and 2nd	Between 2nd and 3rd	Between 3rd and 4th	Between outer spines	Valve length
Mean (mm.)	0.28	0.40	0.60	0.74	2.66	2.66
(var.)	(0.0017)	(0.00069)	(0.0065)	(0.0125)	(0.190)	(0.266)
n.	30	30	27	5	30	30

TABLE 15. Statistics of the distances between hinge-spines (numbered outwards from the umbo) of *Globosochonetes parseptus* gen. et sp. n., together with the total distance between the outer pair of spines and the length of the valves.

TABLE 16

\bar{l} mm. (var.) = 2.15 (0.266)
r = 0.946

\bar{w} mm. (var.) = 2.61 (0.960)
a (var.) = 1.315 (0.00371)

TABLE 16. Statistics of length (\bar{l}) and maximum width (\bar{w}) of 51 pedicle valves of *Globosochonetes parseptus* gen. et sp. n.

TABLE 17

\bar{l} mm. (var.) = 2.30 (0.272)

\bar{l} mm. (var.) = 2.30 (0.272)

\bar{w} mm. (var.) = 2.89 (0.370)

\bar{th} mm. (var.) = 0.99 (0.060)

r = 0.959

r = 0.895

a (var.) = 1.171 (0.00427)

a (var.) = 0.469 (0.00169)

TABLE 17. Statistics of length (\bar{l}), maximum width (\bar{w}) and thickness (\bar{th}) of 28 shells of *Globosochonetes parseptus* gen. et sp. n.

TABLE 18

\bar{l} mm. (var.) = 1.98 (0.216)

\bar{s} mm. (var.) = 0.52 (0.0147)

r = 0.729

a (var.) = 0.263 (0.00088)

TABLE 18. Statistics of valve length (\bar{l}) and the distance between the anterior ends of the accessory septa (\bar{s}) of 39 brachial valves of *Globosochonetes parseptus* gen. sp. n.

Subfamily RUGOSOCHONETINAE Muir-Wood 1962

Genus RUGOSOCHONETES Sokolskaja 1950

TYPE SPECIES. *Orthis hardrensis* Phillips 1841, pars, by original designation of Sokolskaja (1950: 23).

DISCUSSION. Diagnosis of the genus depends upon an understanding of *R. hardrensis*. The species was discussed by Muir-Wood (1962) who selected a lectotype

from amongst the Phillips specimens from Hardraw, Wensleydale, now at the University Museum, Oxford, (E.1571). Neither this specimen nor the remaining Hardraw specimens at Oxford are particularly well preserved, being moulds or somewhat crushed specimens in shale. The lectotype, and two other specimens (E.1577, 1578), show distinct lobate areas on either side of the mid-line presumably accentuated by sediment compaction and slight crushing of the shell. These areas exactly match elevated regions seen on the dorsal interior of a specimen from Ray Gill, near Hawes, Wensleydale (Geol. Surv. Mus. 95131), which are assumed to mark the regions enclosed by the spirulophe. Further collecting is required to ascertain whether this dorsal morphology is a consistent and specific feature. The similarly sized specimens E.1569 (Univ. Mus. Oxford) and BB.41147 (British Museum (Nat. Hist.)), figured by Muir-Wood (1962), show dorsal interiors without distinguishable brachial areas and such specimens may prove to be distinctive.

In comparing the Fermanagh rugosochonetids with the types of *R. celticus* it became apparent that the specimens assigned by Muir-Wood to this species belong to three distinct groups. The holotype (BB.41145) from Flintshire, North Wales, (Pl. 7, figs. 28-31) together with other specimens from Flintshire and elsewhere in Britain are distinguishable by their clear and fine ribs. Five, 25 and 8 specimens have respectively 4, 5 and 6 ribs per mm. at 4 mm. from the ventral umbo. Muir-Wood (1962 : 69) mentions a coarsely ribbed variant and these valves were figured as being conspecific. Three, 10 and 4 specimens have respectively 2, 3 and 4 ribs per mm. at 4 mm. from the ventral umbo (e.g. B.53892 and 68475 in Brit. Mus. (Nat. Hist.) (Pl. 8, figs. 2-5), and although they have been found at the same localities as the fine ribbed *R. celticus* s.s., appear to have other distinctive features. The coarse ribbed shells have more prominent rib apertures and a relatively longer ventral median septum than have the finely ribbed group, and the ventral adductor scars are distinctive in being slightly raised above the floor of the valve.

The *R. celticus* picture is further complicated by specimens from Northumberland and Fifeshire which are poorly ribbed (e.g. B.42046, BB.41100-01 and B.53929-34) (Pl. 8, figs. 6-9). While the rib frequency is consistent with *R. celticus* s.s., the ribbing is absent postero-laterally, near the posterior margin, and commonly replaced anteriorly, after a valve length of 7-9 mm., by irregular but prominent "growth-lines". This anterior region is commonly infested by boring organisms and it may be that an ecological factor effected the growth of these shells. They further differ by their slightly greater width, relative to length; flatter umbo and smoother ventral diductor scars than in *R. celticus* s.s. Owing to the poorly developed ribbing, the internal valve margins are not strongly crenulated.

The distinctions between *R. celticus* and *R. hardrensis* are slight. Muir-Wood (1962 : 70) says that the former is larger, more convex in profile, has spines extending from the hinge at a lower angle, and "has slight internal differences" from *R. hardrensis*. The few complete shells assigned to *R. hardrensis* from the Hardraw or Gayle shales of Wensleydale that are available for study (Geol. Surv. Mus. 93151-93152; Brit. Mus. (Nat. Hist.) B.80965-80966, and BB.52661-52666) are almost indistinguishable from the holotype of *R. celticus*. One Wensleydale specimen in the Geological Survey Museum (93152) is 0.5 mm. longer and wider than the holotype

of *R. celticus* and differs in shape by being almost 20% thicker! The rib frequency is 25 in 5 mm. at 5 mm. from the ventral umbo in both specimens. The difficulty in comparison lies in the poor preservation of the *R. hardrensis* lectotype and in deciding if this specimen is conspecific with the *R. celticus*-like Wensleydale specimens. If this were so *R. celticus* would be a junior synonym of *R. hardrensis*. However, until a large localised collection can be studied to enable valid comparisons to be made, the two species must remain. Within *R. celticus* Muir-Wood distinction should be drawn between the finely ribbed holotype group; the coarsely ribbed group and those with poorly developed ribbing. These groups may well warrant at least subspecific designation.

Rugosochonetes silleesi sp.n.

(Pl. 8, figs. 10-27; Text-figs. 42-50)

DIAGNOSIS. *Rugosochonetes* with strongly convex pedicle valve and prominent umbo; multicostellate with 6 ribs per mm., 4 mm. from dorsal umbo, rib apertures present.

DESCRIPTION. Outline semielliptical with length about two-thirds maximum width, hinge-line straight; shell unequiconcavo-convex with rounded ventral umbo extending beyond hinge-line, thickness approximately one-third hinge width; hinge spines extend posteriorly at about 30° to median plane, seven pairs on adult valves; multicostellate, ribs rounded, as wide as interspaces; about twenty-five costae, costellae commonly added by intercalation on brachial valve and by dichotomy on pedicle valve; about six ribs per 1 mm. width, 4 mm. antero-medianly of dorsal umbo, rib apertures sparsely developed; fine concentric growth-lines indistinct; ventral interarea anacline to orthocline, short, delthyrium quadrate to triangular, pseudodeltidium apical, much reduced; dorsal interarea hypercline, reduced, small chilidial plates flank notothyrium; teeth set slightly below and parallel to plane of interarea, grooved on ventral surfaces; median septum high umbonally, thickened below delthyrial apex, in adult shells extending one-third valve length as low ridge; ventral muscle field flabellate, adductor scars pear-shaped, diductor scars elongately triangular, bounded postero-laterally by distinct shell thickening; hinge spines commonly communicating internally through oblique canals; cardinal process bilobed, poorly differentiated, myophores dorsally directed, V-shaped and incised; cardinal process laterally supported by socket ridges at about 20° to hinge-line, which enclose well defined sockets anteriorly; alveolus well defined; median septum extends about one-half length of adult valve; lateral septa prominent anteriorly, disposed at 30° to mid-line, and extending for about one-third length of adult valve; dorsal muscle field indistinct, posterior and anterior adductor scars pear-shaped and oval, separated by posterior ends of lateral septa; both valves internally ornamented by anteriorly directed radial rows of tubercles corresponding to external interspaces and pseudo-punctation, valve margins internally ribbed.

MEASUREMENTS (in mm.):

		length	width
HOLOTYPE.	Complete shell (BB.52758)	9·6	12·6
PARATYPES.	Complete pedicle valve (BB.52759)	9·6	12·7
	Incomplete pedicle valve (BB.52760)	—	13·0
	Complete brachial valve (BB.52761)	9·1	14·4
	Incomplete brachial valve (BB.52762)	10·3	—
	Complete brachial valve (BB.52763)	2·8	3·9
	Complete brachial valve (BB.52764)	7·7	11·8
	Complete shell (BB.52766)	9·8	13·0
	Complete pedicle valve (BB.52765)	7·0	8·9
	Incomplete pedicle valve (BB.52767)	3·7	c. 4·9
	Complete shell with pedicle sheath (BB.52768)	1·6	2·0
	Shell crushed in shale (BB.52769)	c. 11·1	c. 17·2
	Shell crushed in shale (BB.55784)	c. 11·0	c. 17·2
	Incomplete shell (BB.52770)	4·7	—

TYPE LOCALITY. Sillees River, about 300 yds. east of Bunnahone Lough (low D zone)

DISCUSSION. The Fermanagh material is in general accordance with several features described or illustrated by Muir-Wood for *R. celticus* (1962 : 68). However, the shells only rarely reach the dimensions given by her, "about 19 mm. wide, 14 mm. long, and 3 mm. thick", in the shales below the silicified limestone horizon which yields the present sample. More important distinctions are in the proportions of size and ribbing. Selecting 38 shells of *R. celticus* s.s. (i.e. holotype and conspecific specimens with the fine ribbing taken from a number of localities, in the British Museum (Nat. Hist.) collections) 5, 25 and 8 specimens have respectively 4, 5 and 6 ribs per 1 mm. width, 4 mm. antero-medially. This compares with 6, 20 and 3 specimens of *R. silleesi* having respectively 5, 6 and 7 ribs per mm. (Table 21). The thickness of the shell, compared to length, is consistently greater in *R. silleesi* as a result of the deeper, more prominently rounded ventral umbo; the relative shell length is also slightly greater. The shell outline underwent little change during growth other than becoming relatively wider, although the cardinal extremities were usually obtuse and only rarely represented the widest part of the shell. This variability seems to have resulted from an acceleration of growth in a lateral direction during the formation of each pair of spines. The spines, which number seven pairs in adult shells, arose with fairly regular spacing along the posterior margin of the ventral interarea (Table 22). It is frequently impossible to distinguish the sites of the first formed spines, and for this reason measurements were always taken from the mid-line of the valve to the second pair of spines. However, when the first pair were distinguishable, measurements were made and range from 0·35 to 0·6 mm., with a modal value of 0·4 mm. The spines become stronger laterally, the sixth pair commonly being about 0·2 mm. in diameter. Most spines are inserted obliquely to the posterior margin of the valve but almost immediately

continued to grow posteriorly at a high angle from the posterior margin of the valve. At each stage of growth the spines were posteriorly projecting so that in the adult shell the oldest, median spines, are nearly dorsally directed, while the youngest, lateral spines, project posteriorly (Text-fig. 42). This indicates the degree of rotation relative to the hinge-line during growth. Most commonly the spines retained hollow connection to the valve interior throughout adulthood (Pl. 8, fig. 22). The

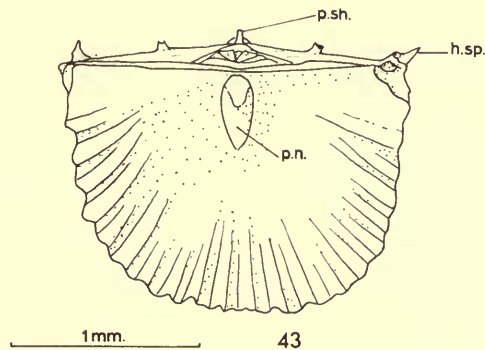
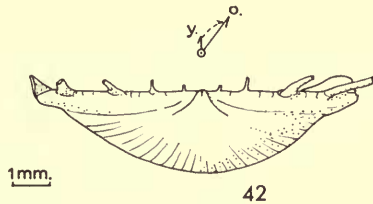


FIG. 42. Posterior view of a rugosochonetid shell showing the way in which rotation of the commissural plane relative to the horizontal led to a swing in the orientation of the hinge-spines from being dorsally directed, medianly, to posteriorly directed, laterally, in adult shells; *y* and *o* indicate the spine orientation relative to the hinge-line axis of the spines formed in youth and old-age respectively.

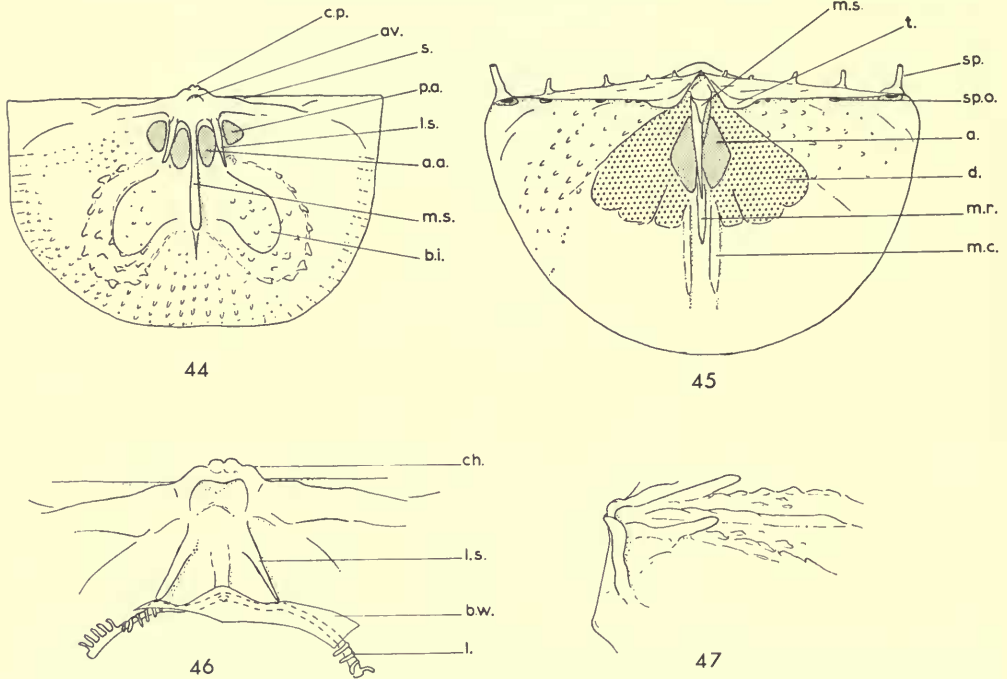
FIG. 43. Illustration of a young rugosochonetid shell viewed postero-dorsally; *h.sp.*, hinge-spine; *p.n.*, protegular node; *p.sh.*, pedicle sheath projecting from the tip of the ventral umbo. The cardinal process is bilobed and a rudimentary chilidium is commonly distinguishable.

lateral two or three pairs of spines have broad direct openings to the interior, antero-ventral of the hinge-line, while the median three or four pairs retain connection by obliquely disposed canals through the interarea, so as to open ventro-laterally of the teeth. In a shell 13.0 mm. wide along the hinge-line, the second and third pairs of spines have canals, 0.8 mm. long, running through the interarea at about 70° to the mid-line.

The convexity of the pedicle valve is regular in the mid region, but there is flattening towards the cardinal extremities to form small ears. The brachial valve is flat for the first 1.0 mm., around the prominent protegular node (Text-fig. 43).

Beyond this length concavity of the valve is gentle and regular so as to meet the pedicle valve towards the anterior margin as a short trail.

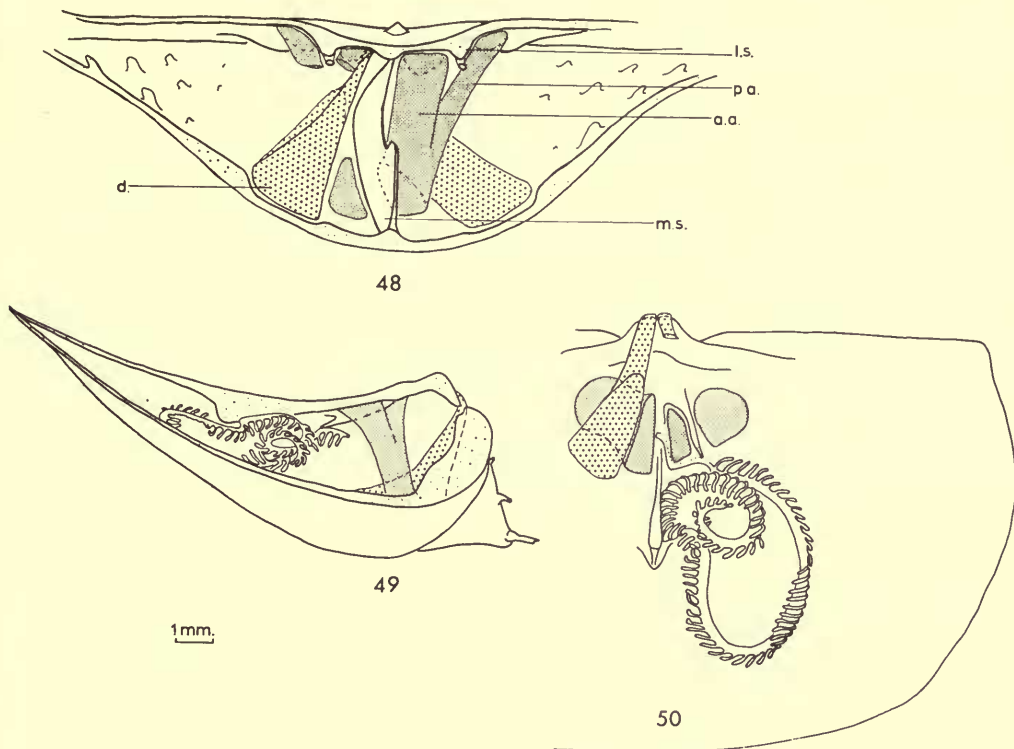
The radial ornament is equally conspicuous on both valves, although obscure for about the first 1 mm. of both valves. The ribs are prominent, rounded and of much the same wave-length as the interspaces, each one slightly increasing in size towards the anterior margin. Table 23 shows the range in the number of costae observed on



FIGS. 44-47. Illustrations of principal internal morphological features of chonetids; brachial valve (Fig. 44), pedicle valve (Fig. 45); a reconstruction of the postero-median segment of the stylized lophophore and body wall supported by the lateral septa (Fig. 46); and a lateral view of the lateral septa (Fig. 47), *a.a.*, anterior adductor scar; *a.*, ventral adductor scar; *av.*, alveolus; *b.i.*, brachial impression; *b.w.*, body wall; *ch.*, chlidium; *c.p.*, cardinal process; *d.*, ventral diductor scar; *l.*, stylized lophophore; *l.s.*, lateral septum; *m.c.*, trace of a mantle canal; *m.r.*, median ridge; *m.s.*, median septum; *p.a.*, posterior adductor scar; *s.*, socket; *sp.*, spine; *sp.o.*, internal spine opening; *t.*, tooth.

brachial valves. The number counted on pedicle valves is consistently comparable, and within the same range for four. On the brachial valve costellae are most commonly added by intercalation; this is almost invariably so over the median region of the valve, but on the flanks sporadic dichotomy of the ribs is usual. Intercalation is rare on the pedicle valves and dichotomy is the usual method of branching (Table 24). Thus the ribbing is complimentary and ventral dichotomy is usually accompanied by dorsal intercalation during growth. Muir-Wood (1962 : 9) wrote of the "elongate-trigonal perforations" seen on the ribs of "most chonetids", as being

the "base of small hollow spinules which were very fine and delicate and are rarely preserved in place". These apertures are irregularly and sparsely distributed on the ribs of *R. silleesi* as anteriorly directed arches temporarily terminating the rib. Anteriorly the rib regained its normal dimensions over a distance of less than 0.5 mm. (Pl. 9, figs. 1, 2). The same sort of structure is to be seen on the ribs of *Schizophoria* and *Rhipidomella* from the same locality. The apertures were formed



FIGS. 48-50. Stylized reconstructions of the musculature and inferred position of the diagrammatic lophophore in *Rugosochonetes silleesi* sp. n. as seen in transverse section from the anterior (Fig. 48), in longitudinal section (Fig. 49), and the brachial valve interior (Fig. 50), *a.a.*, anterior adductor muscle; *d.*, diductor muscle; *l.s.*, lateral septum with its prolongation showing as a discrete position of shell between the dorsally divided adductor muscles; *m.s.*, ventral median septum; *p.a.*, posterior adductor muscle.

by the temporary retraction or sagging of the mantle edge from the inner shell surface of the rib so that deposition ceased to form a rib until the mantle had once again become folded. Muir-Wood has referred to the taxonomic importance of these "spinulus". Certainly there seems to be a genetical control within brachiopods as a whole, governing the formation of these apertures; a control which is of systematic importance amongst Lower Palaeozoic orthaceans and enteleteans.

The ventral beak of young shells is grooved, in a similar way to that of *Globosochonetes*, but a pedicle sheath is only rarely preserved (Pl. 8, fig. 26). The median

septum was developed from the earliest stages, but only in shells longer than about 5 mm. is the median ridge developed anteriorly of the high umbonal septum.

Within the dorsal valve, the lateral septa, or anderidia of Sadlick (1965 : 157) became prominent in valves more than 5 mm. long, prior to which the septa are little more than raised tuberculate regions with a posteriorly placed ridge of about 0.3 mm. In adult shells the septa developed anteriorly forming distinct prongs. From their anterior ends indistinct reniform areas, enclosed by a slight ridge or by tubercles, can be seen extending beyond the median septum for about two-thirds of the valve length (Text-fig. 44). The dorsal median septum is low and flattened, except anteriorly (Pl. 8, fig. 23). This flattening did not result from restriction within the body cavity of the shell as the valves are well separated in this region. The lateral septa (anderidia) are thought to have given support to the posterior ends of the primary loop of the spirolophore (Text-fig. 46), which was itself partly supported by the median septum and partly from the reniform markings antero-lateral of the median septum. Such an arrangement of the brachial apparatus would have been similar to that illustrated by Williams (1956) in fig. 5 (6) for *Productus* s.s. Text-figs 48-50 show the inferred gross anatomy of the species. If this interpretation is correct, the prolongations of the lateral septa (anderidia) protuded anteriorly of the visceral cavity, as defined anteriorly by the inferred paths of the adductor muscles. It is envisaged that the prolongations supported the anterior body wall at the points from which the lophophore was supported. Sadlick (1965 : 158) describes the anderidia as being in the coelomic cavity and well behind the body wall, and argues

TABLE 19

\bar{l} mm. (var.) = 6.11 (8.7144) \bar{w} mm. (var.) = 8.02 (15.213) $r = 0.992$ a (var.) = 1.321 (0.00073)	\bar{l} mm. (var.) = 6.11 (8.7144) \bar{th} mm. (var.) = 2.29 (2.0567) $r = 0.920$ a (var.) = 0.486 (0.00110)
\bar{th} mm. (var.) = 2.29 (2.0567) \bar{x} mm. (var.) = 7.08 (12.039) $r = 0.972$ a (var.) = 2.419 (0.00847)	

TABLE 19. Statistics of length (\bar{l}), maximum width (\bar{w}), thickness (\bar{th}) and width of hinge-line (\bar{x}) of 40 shells of *Rugosochonetes silleesi* sp. n.

TABLE 20

\bar{l} mm. (var.) = 6.77 (1.422)
\bar{s} mm. (var.) = 3.17 (0.739)
$r = 0.959$
a (var.) = 0.721 (0.00350)

TABLE 20. Statistics of length (\bar{l}) and length of the median septum (\bar{s}), measured from the hinge-line, of 14 brachial valves of *Rugosochonetes silleesi* sp. n.

TABLE 21

No. of ribs	5	6	7	8
At 2 mm. from umbo	1	11	16	2
At 4 mm. from umbo	6	20	3	0

TABLE 21. Ribs counted per 1 mm. width at distances of 2 mm. and 4 mm. antero-medially from the dorsal umbo of *R. silleesi* sp. n.

TABLE 22

Distances between spines	Umbo and 2nd	2nd and 3rd	3rd and 4th	4th and 5th	5th and 6th	6th and 7th
Mean (mm.)	0.90	0.74	1.018	1.22	1.26	1.35
(Var.)	(0.01214)	(0.0182)	(0.0395)	(0.0157)	(0.0257)	
N	29	28	22	15	8	2

TABLE 22. Distribution of hinge-spines. Distances measured from the mid-line to the second spine and subsequently between additional spines of *R. silleesi* sp. n.

TABLE 23

No. of costae on dorsal valves	20-23	24-27	28-30
No. of specimens	4	18	6

TABLE 23. The number of costae counted on 28 dorsal valves of *Rugosochonetes silleesi* sp. n.

TABLE 24

	Dichotomy			Intercalation
	Flanks	Median sector	Both	
Brachial valves	19	2	2	30
Pedicle valves			30	4

TABLES 24. Scoring for the method by which costellae were added on 53 brachial valves and 34 pedicle valves of *R. silleesi* sp. n.

that they could not have been used for lophophore attachment. While this is agreed, nevertheless it is considered that these ridges developed functionally as posterior supports to the lophophore and that in life the anteriorly projecting processes were probably prominent in adult shells. Having restricted the anderidia to the coelomic cavity Sadlick can hardly suggest that "long anderidia undoubtedly helped form a channel for inhalent currents" (1965 : 158).

Rugosochonetes delicatus sp. n.

(Pl. 9, figs. 3-15, Text-figs 51, 52)

DIAGNOSIS. Gently concavo-convex *Rugosochonetes* with flattened ventral umbo, thin-shelled; finely and indistinctly multicostellate with few rib apertures; muscle scars obscurely developed.

DESCRIPTION. Outline subsemicircular, about two-thirds as long as wide, greatest width at straight hinge-line with poorly defined triangular ears; profile concavo-convex, pedicle valve evenly convex, umbo flattened, not extending beyond hinge-line, thickness one-quarter to one-third length, body cavity narrow; adult shells with four pairs of hinge-spines at 30° to 40° from mid-line; multicostellate, ribs low and rounded, umbones smooth, costellae rarely added by dichotomy and intercalation, commonly 7 ribs per mm. width, 2 mm. or 4 mm. antero-medially of pedicle umbo; rib aperture sparse, growth-lines indistinct; ventral interarea apsacline to orthocline, short, delthyrium open, pseudodeltidium reduced; dorsal interarea one-third length of ventral interarea, chilidial plates small, arcuate; teeth subparallel to interarea, slightly crenulated distally; median septum short but high, extending about 1 mm. across ventral umbo and separating indistinct flabellate muscle field; first 2 pairs of spine openings deflected laterally by semiconical screens of secondary shell; cardinal process lobes more or less fused medianly, myophore V-shaped, directed postero-dorsally and fused proximally; deep alveolus flanked by socket ridges at about 20° to hinge-line and extending about one-third its width; lateral ridges short and low posteriorly; shell substance thin, pseudopunctate.

MEASUREMENTS (in mm.):

		length	width
HOLOTYPE.	Complete shell (BB.52771)	6.5	8.5
PARATYPES.	Complete pedicle valve (BB.52772)	6.5	9.3
	Incomplete pedicle valve (BB.52773)	—	8.3
	Complete damaged shell (BB.52776)	3.6	c. 5.8
	Complete shell (BB.52774)	c. 5.0	7.6
	Complete pedicle valve (BB.52775)	5.0	6.6

TYPE LOCALITY. Sillees River, about 300 yds east of Bunnahone Lough (Low D zone).

DISCUSSION. The species is similar in estimates of relative length and thickness to *R. silleesi* (Tables 19, 25) with which it occurs. and the two are probably closely

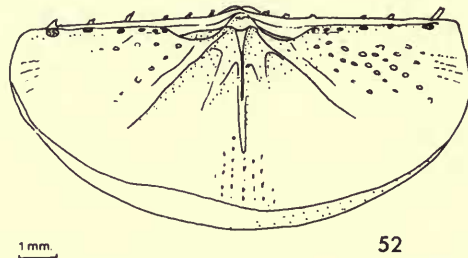
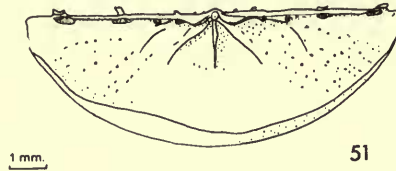
related. In other respects, however, there are persistent clear differences. Thus, *R. delicatus* differs from *R. silleesi* in having a much flatter ventral umbo which does not project beyond the hinge-line, which constitutes the greatest width of the shell. The radial ornament, although of similar frequency, is less prominent, the ribs being low and costellae added on the pedicle valve by intercalation and dichotomy rather than almost entirely by dichotomy. The rows of tubercles are uniformly delicate over the entire ventral interior, about 4 occurring per mm. on the lateral flanks, whilst in this region of *R. silleesi* the tubercles are about twice the size with a frequency of 2 or 3 per mm. The dorsal median septum is ill defined and perhaps never fully developed. The body cavity is smaller and the shell substance thinner.

The poorly defined ribbing and its absence close to the posterior margin is similar to the ornamentation of *R. hindi* Muir-Wood from the H zone of Cheshire, and to the poorly ribbed specimens of *R. celticus* Muir-Wood typical of the low E zone of Northumberland. However, the Fermanagh specimens differ from the former species in being concavo-convex, having fewer spines per unit length of hinge-line and in having 7 or 8 ribs per mm. at 4 mm. from the umbo as compared to 5 or 6 per mm. in *R. hindi*. The frequency of ribbing on 5, 13 and 5 specimens attributed to *R. celticus* from Northumberland is 4, 5 and 6 ribs per mm respectively. 4 mm. from the umbo. This frequency is comparable to that of *R. celticus* s.s., but is coarser than that of the two Fermanagh species *R. silleesi* and *R. delicatus*.

The brephic shell was furnished with a supra-apical pedicle sheath (Pl. 9, fig. 14), extending ventro-posteriorly, which arose from the tip of the pedicle beak and posterior to the shallow V-shaped groove across the young shell. During growth each pair of hinge-spines was inserted at fairly regular intervals and projected posteriorly in the commissural plane at the time of their growth. As growth proceeded the commissural plane rotated clockwise relative to the substratum (as viewed laterally with the umbo to the left) so that adult shells have their lateral spines directed posteriorly and their median, early formed spines, project dorsally as in *R. silleesi* (Text-fig. 42). Like *R. silleesi*, the spines retain their connection to the interior, but unlike that species, the interarea is only slightly thickened so that instead of oblique canals maintaining connection, localized deposits of secondary shell deflect the internal openings laterally to positions comparable to those of *R. silleesi* (Text-figs 51, 52). This deflection became less pronounced during growth so that younger spines have more direct openings to the interior. A valve 9.3 mm. wide has its first formed spines 0.5 mm. from the mid-line, but these do not open to the interior for a distance of 1.2 mm. from the mid-line; at this distance the second spines occur and these open internally 1.7 mm. from the mid-line.

The slight amount of secondary shell deposition has resulted in poorly developed internal markings. The ventral muscle field has slight postero-lateral thickenings at its margin, but the median septum is rarely continued as a median ridge. Only two cardinalia are available for study and these have well developed socket ridges at about 20° to the hinge-line, extending about one-third of the hinge-width; the lateral septa (anderidia) are clearly distinguishable, having raised prolongations anteriorly which are considered to have supported the posterior sections of the lophophore. There is no apparent indication of the development of a dorsal median septum,

and it is certainly absent at a hinge width of about 8 mm. However, preservation of brachial valves is not sufficiently good to be able to say with certainty that no septum existed in old shells, especially as it is a structure which developed late in the ontogeny of *Rugosochonetes*.



FIGS. 51-52. Illustrations of the pedicle valve interior of *Rugosochonetes delicatus* sp. n. (Fig. 51) and *R. silleesi* sp. n. (Fig. 52) showing the difference in the internal spine openings.

TABLE 25

\bar{l} mm. (var.) = 5.26 (1.367)	\bar{l} mm. (var.) = 5.26 (1.367)
\bar{w} mm. (var.) = 7.63 (2.341)	\bar{th} mm. (var.) = 1.58 (0.315)
$r = 0.980$	$r = 0.803$
a (var.) = 1.309 (0.00404)	a (var.) = 0.480 (0.00481)

TABLE 25. Statistics of length (l), maximum width (w) and thickness (th) of 19 pedicle valves of *Rugosochonetes delicatus* sp. n.

TABLE 26

Ribs	6	7	8	9
at 2 mm.	4	9	3	3
at 4 mm.	4	8	7	1

TABLE 26. Number of ribs counted per mm. width at 2 mm. and 4 mm. antero-medially of the ventral umbo of *R. delicatus* sp. n.

Rugosochonetes transversalis sp. n.

(Pl. 9, figs. 16-25)

DIAGNOSIS. Wide *Rugosochonetes* with semi-elliptical outline, low rounded costellation; median ridges of cardinal process subparallel and narrowly separated; socket ridges prominent and divergent from hinge-line.

DESCRIPTION. Outline transversely semi-elliptical, about one-half as long as wide, umbo flattened, not extending beyond hinge-line which constitutes greatest width of shell; profile concavo-convex, regular, about one-third as deep as long, body cavity narrow, commonly slightly sulcate; hinge-spines irregularly placed at high angle; multicostellate, ribs low rounded with rare apertures, costellae added by dichotomy on both valves, with about 3 ribs occurring per mm. width, 4 mm. antero-medially from ventral umbo; growth lines indistinct; ventral interarea more or less orthocline, delthyrium about one-third closed by highly arched apical pseudo-deltidium; dorsal interarea orthocline to apsacline, about one-half length of ventral interarea, notothyrium with U-shaped chilidium; teeth diverging slightly from interarea; short high median septum separating elongate oval adductor scars, with flanking trigonal diductor scars; median ridge may extend anteriorly from septum for 2 or 3 mm.; two low ridges extend beyond median ridge from anterior ends of adductor scars for about two-thirds valve length (possibly traces of *vascula media*); cardinal process rather wide, median muscle ridges narrowly separated, lateral ridges divergent giving quadrified postero-dorsal surface; sockets deep, anteriorly bordered by prominent socket ridges extending about one-quarter hinge width; adult median septum partly fills alveolus, extending nearly one-half valve length, broad and low, anteriorly raised; lateral septa diverge at 25° from mid-line, and separate elongate oval anterior adductor scars from wider trigonal posterior scars; internally radially tuberculate except postero-laterally; shell substance pseudopunctate.

MEASUREMENTS (in mm.):

		length	width
HOLOTYPE.	Complete shell (BB.52778)	13.5	c. 23.0
PARATYPES.	Incomplete pedicle valve (BB.52779)	c. 11.0	c. 22.0
	Incomplete pedicle valve (BB.52781)	5.5	—
	Complete brachial valve (BB.52783)	10.0	19.5

TYPE LOCALITY. Sillees River, about 300 yds east of Bunnahone Lough (Low D zone).

DISCUSSION. The radial ribbing is almost as wide as that found within *Plicochonetes*, as emended by Muir-Wood (1962 : 82), but differs in being poorly defined with low indistinct ribs. Branching is not common but almost invariably by dichotomy. Table 28 shows the distribution of costellation on pedicle valves. Growth lines are indistinct and may be impossible to distinguish on the silicified material. This poorly defined ornamentation cannot be attributed to abrasion, prior to silicification, as delicate structures, such as hinge spines and the pseudodeltidium are

preserved, and the concave brachial valves would have been well protected. About one-half of the pedicle valves show sporadic concentric lamellae, probably indicating some irregular retardations of growth. Eight out of twelve shells have a slight median sulcation in their pedicle valves which dies out towards the anterior margin. This folding is even less marked on the brachial valves. Currie (1937 : 423) pointed out that a median sulcation of *Chonetacea* arose in the mid Carboniferous and it may be that the slight sulcation seen on several of the Fermanagh shells is an indication of this trend.

In outline *R. transversalis* is similar to *C. laguessiana* de Koninck mut. θ Hind from the Gin Mine Marine Band, N. Staffs. (Brit. Mus. (Nat. Hist.) B.47309), but this shell is more finely ribbed, and in this respect is comparable to *R. celticus* s.s. It has about 8 spines in 10 mm. on either side of the umbo which contrasts with 5 or 6 spines in the same distance on the Fermanagh shells. In *R. transversalis* most of the spines retain internal openings, the more medianly placed spines having oblique canals leading to their openings which are lateral of the teeth. The internal surfaces of the ears, and regions immediately anterior of the interareas, are not tuberculate, but the ear regions are irregularly pitted. In old shells, the radial rows of tubercles tend to coalesce into low ridges with the tips of the tubercles still protruding from their crests. The ventral median septum terminates posteriorly in a thickened region between the bases of the teeth and below the apex of the delthyrium, but without the distinctly node-like callus of *R. silleesi*.

The dorsal median septum is typical for the genus in its late development, and the lateral septa are again prominent anteriorly, protruding from the valve floor to the inferred position of the body wall. Like the ventral valve, tuberculation is confined to the mid and lateral regions, and towards the cardinal extremities the pair of slight knobs probably assisted in the articulation of this long-hinged species. Brachial ridges are not clearly distinguishable.

TABLE 27

l mm. (var.) = 10.70 (9.6943)	l mm. (var.) = 10.70 (9.694)
\bar{w} mm. (var.) = 18.78 (40.640)	\bar{th} mm. (var.) = 3.77 (4.257)
$r = 0.578$	$r = 0.770$
a (var.) = 2.048 (0.0465)	a (var.) = 0.663 (0.0208)

TABLE 27. Statistics of length (l), maximum width (w) and thickness (th) of 8 shells or pedicle valves of *Rugosochonetes transversalis* sp. n.

TABLE 28

Ribs	3	4	5
at 2 mm.	0	6	5
at 4 mm.	9	3	0

TABLE 28. Number of ribs counted in 1 mm. width at 2 and 4 mm. antero-medially from the pedicle umbo of *Rugosochonetes transversalis* sp. n.

Genus *PLICOCHONETES* Paeckelmann, 1930

TYPE SPECIES. *Chonetes buchianus* de Koninck, 1843, by original designation of Paeckelmann (1930 : 222).

Plicochonetes buchianus (de Koninck)

(Pl. 9, figs. 27-32)

DIAGNOSIS (emended). Strong concavo-convex *Plicochonetes* with narrow body cavity; prominent rounded ribs, not developed postero-laterally; small pseudo-deltidium and chilidial plates present; dorsal median septum short and low.

DESCRIPTION. Outline subsemicircular with straight hinge-line at widest part of shell, about two-thirds as long as wide; ears well developed and smooth; profile concavo-convex with narrow body cavity, shell about one-half as deep as long; radial ornament prominent and evenly developed from about 16 costae with rare additions of ribs by branching on pedicle valves and intercalation on brachial valves, about 5 ribs per 2.5 mm. at 4 mm. from ventral umbo, rib-apertures sparsely developed on both valves; growth lines finely developed; ventral interarea concave, more or less orthocline, delthyrium closed apically by small arched pseudodeltidium; at least seven pairs of hinge spines subparallel to mid-line; dorsal interarea hypercline with notothyrium similarly sized to delthyrium and flanked by prominent chilidial plates; teeth suboval in outline; short high median septum extending as low ridge between elongately oval adductor scars; diductor scars poorly impressed; cardinal process bilobed and medianly fused, external face quadrifid with prominent median muscle boundaries separated by narrow groove; socket ridges extending about one-third hinge-line width; median septum low and broad, raised anteriorly and extending about one-quarter valve length, but continued as short ridge; lateral septa at 25° to 30° from mid-line, commonly prominent anteriorly; brachial impressions lobate, extending about three-fifths valve length and disc width; shell substance thin.

MEASUREMENTS (in mm.):

	length	width
Complete shell (BB.52917)	7.8	12.8
Incomplete brachial valve (BB.52918)	10.6	c. 16.0
Incomplete brachial valve (BB.52919)	6.9	—

DISCUSSION. The species is rarely found in the limestones from Co. Fermanagh, but a few well preserved specimens warrant discussion.

The genus was inadequately described by Paeckelmann (1930). In her description of the genus Muir-Wood (1962 : 82) makes no mention of the presence of chilidial plates. These are well developed arching the lateral flanks of the external face of the cardinal process so as partially to obscure the lateral muscle boundary ridges (Pl. 9, fig. 30). The plates are barely fused medianly, but were well developed when the

valve was 6 mm. long. The presence of a well defined apical pseudodeltidium in the present material indicates that this structure may be commoner on well preserved material than has been thought. This structure, together with the chilidial plates should be noted within a diagnosis of *Plicochonetes*.

The correspondence between the ribbing of the brachial and pedicle valves is indicated by the way in which costellae are commonly added by intercalation on the brachial valve in a position opposite to a branched rib on the pedicle valve. An example of this can be seen on the shell illustrated on Pl. 9, figs. 29, 30. This is considered to be a common feature of ribbing, and is a necessity for a close fit of the anterior margin, but is difficult to demonstrate on more finely ribbed groups.

Rib apertures are developed both on the ribs and sparsely on the smooth ears in a radial fashion. These structures are more fully discussed under *Rugosochonetes*.

In common with other chonetaceids, the lateral septa developed at an early stage, prior to the differentiation of the median septum or clear development of the adductor scars (Pl. 9, fig. 31). Their prominence indicates a functional importance and their prolonged anterior extremities probably assisted in the support of the lophophore at the body wall as in *Rugosochonetes*.

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